

# Agriculture, Ecosystems and Environment

## A predator in need is a predator indeed: generalist arthropod predators function as pest specialists at the late growth stage of rice

--Manuscript Draft--

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<b>Manuscript Region of Origin:</b>	TAIWAN
<b>Abstract:</b>	Biocontrol, using natural enemies for pest control, has a long history in agriculture. It has received a surge of interest in the recent Anthropocene because of its potential as a valuable tool for sustainable agriculture. To solve a long-standing puzzle in biocontrol—how well the ubiquitous generalist arthropod predators (GAPs) function as biocontrol agents—this study aimed to 1) quantify the diet composition of GAPs at each crop stage using stable isotope analysis, 2) examine the consistency of GAPs in pest consumption over years, and 3) investigate how abiotic and biotic factors affect pest consumption by GAPs. Specifically, we sampled arthropod prey and GAPs in subtropical organic and conventional rice farms over crop stages (seedling, tillering, flowering, and ripening) in three consecutive years. Among our field-collected samples, 352 arthropod predator and 828 prey isotope samples were analyzed to infer predator-prey interactions. Our results show the following: a) The proportion of rice pests in GAPs' diets in both organic and conventional farms increased over the crop season, from 21-47% at the tillering stage to 80-97% at the ripening stage, across the three study years. The high percentage in pest consumption at late crop stages (flowering and ripening) suggests that GAPs can function as specialists in pest management during the critical period of crop production. Regarding individual predator groups, spiders and ladybeetles exhibited distinct dietary patterns over crop stages. b) The high pest consumption by GAPs at late crop stages was similar across years (with different climatic conditions), suggesting a consistency in GAP feeding habits and biocontrol value. c) The proportion of rice pests in GAPs' diets varied with farm type and crop stage (e.g., higher in conventional farms and during flowering/ripening stages). By quantifying the diet composition of GAPs over crop stages, farm types, and years, this study reveals that generalist predators have potential to produce a stable, predictable top-down effect on pests under various environmental conditions. As sustainable agriculture has become increasingly important, incorporating the ubiquitous generalist predators into pest management will likely open a promising avenue towards this goal.
<b>Suggested Reviewers:</b>	James Pryke Associate Professor, Stellenbosch University jpryke@sun.ac.za Expertise: entomology, agroecology, landscape ecology  Nickson Otieno Stellenbosch University neotieno@yahoo.com Expertise: agroecology, stable isotope analysis

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	<p>Eve Roubinet Swedish University of Agricultural Sciences <a href="mailto:eve.roubinet@slu.se">eve.roubinet@slu.se</a> Expertise: predator-prey interactions in agroecosystems</p>



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October 3, 2023

Dear Dr. Audrey Alignier and Editorial Board Members,

Thank you for providing us an option to submit a revised version of our manuscript (AGEE36058) to *Agriculture, Ecosystems and Environment*. We appreciate the constructive comments from you and the reviewers. We have carefully considered each comment, and our point-by-point responses are provided in this letter. Please note that corresponding revisions do not alter the conclusions of our study.

For clarity, each reviewer's comment is attached below (in gray highlight) and followed by our reply. Line numbers in our reply refer to the revised version with tracked changes unless otherwise mentioned. We submit our revised manuscript with four files:

1. *Manuscript to AEE Main text (track changes) 2023-1002*  
The revision with tracked changes
2. *Manuscript to AEE Main text 2023-1002*  
The revision that accepts all tracked changes
3. *Manuscript to AEE Supplement (track changes) 2023-1002*  
The supplement of this study with tracked changes
4. *Manuscript to AEE Supplement 2023-1002*  
The supplement of this study that accepts all tracked changes

Our study helps solve a long-standing puzzle (the role of generalist predators in pest management) by using stable isotopes to quantify arthropod predators' diet composition over crop stages, farm types, and years. Therefore, our findings should be of interest to a wide range of ecologists, agricultural practitioners, and policy makers. We believe that the revisions based on review comments have improved the quality of this manuscript, and we hope that the manuscript is now suitable for publication in *Agriculture, Ecosystems and Environment*.

Sincerely,

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Professor  
Institute of Ecology and Evolutionary Biology  
National Taiwan University



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Taiwan University



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Sincerely,

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Professor  
Institute of Ecology and Evolutionary Biology  
National Taiwan University

**The following includes our replies to these four sections of comments:**

- Editor's comments
- Reviewers' comments
- Reviewer 1's comments
- Reviewer 2's comments

**Editor's comments**

Thanks for your submission of the manuscript AGEE36058 titled ‘A predator in need is a predator indeed: generalist arthropod predators function as pest specialists at the late growth stage of rice’. This manuscript has been reviewed by two independent experts and their comments are copied below. As you will see, reviewers find the topic interesting however they find too much to criticise in relation to your manuscript which compromises its suitability for publication in AGEE. In particular, objectives and hypotheses are unclear. You should insist on the novelty of your study. The unbalanced design is questionable. More importantly, the method you used appears inappropriate : pest consumers were pooled at a taxonomic level rather too coarse (order) adequate isotopic signature resolution. The absence of intraguild predation is also highly intriguing and questions the significance of the results (especially how efficient spiders are in pest suppression). About the format, I agree with Reviewer#1 that Introduction and Discussion are excessively long. For all these reasons, I've resolved to decline the work with the option to resubmit. Should you ultimately choose to resubmit to AGEE, the expectation is that the commentary would be carefully and thoroughly accounted for in the revised manuscript.

**[Reply]** We thank editor's constructive comments and briefly summarize our responses below. Details are provided in our point-by-point responses to reviewers' comments.

- 1) *Objectives and hypotheses* We have revised the last paragraph of Introduction to clarify our study aim (Line 118), objectives (Line 122), and expectation (Line 127).
- 2) *Unbalanced design* To account for the unbalanced design, we have updated our GLM beta regression by using weights based on the number of observations in each study year. Note that the new analysis (Table 1) does not change the conclusions of our study.
- 3) *Arthropods were pooled* While we identified arthropods to the lowest possible taxonomic level, we grouped them into different trophic guilds for these reasons: a) Trophic guilds represent species using similar resources in food webs and have been widely used in current ecology (Blondel, 2003) (Line 176). b) Stable isotope mixing models may not include too many food sources because it can introduce uncertainties to diet estimates. In our study, three prey sources (rice herbivores, tourist herbivores, and detritivores) should be reasonable compared to the two biotracers ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ). c) The assignment of trophic guilds and pooling of prey samples were based on a combination of literature surveys and k-means clustering of carbon and nitrogen isotope signatures of arthropod samples (Line 185). We now provide a stable isotope biplot to demonstrate the differences among prey sources (Appendix A: Fig. S1). d) Please see more details in our reply to Reviewer 2's comments on Analysis below (*Combing/pooling pest consumers*).

- 4) *The lack of intraguild predation* We understand that intraguild predation (IGP) can play an important role in some communities, especially those with low habitat heterogeneity (Hunter 2009). IGP, however, was not quantified in our analysis due to the limitation of stable isotope mixing models. We acknowledge this limitation in the *Potential caveats of this study* section of our discussion (Line 312 and 419). We also explain that IGP may not be a major concern in our study system because rice plants grow in dense clumps and form a complex structure that could substantially reduce IGP (Line 422). That being said, we now bring up this limitation earlier in our discussion as suggested by Reviewer 1 (Line 312).
  
- 5) *Long introduction and discussion* As suggested, we have cut our introduction and discussion by 112 and 88 words, respectively. These two sections should be more concise now.

#### **Reviewers' comments**

1. Are the objectives and the rationale of the study clearly stated?

Please provide suggestions to the author(s) on how to improve the clarity of the objectives and rationale of the study. Please number each suggestion so that author(s) can more easily respond.

Reviewer #1: Yes

Reviewer #2:

- 1) Yes, the objectives stated but are entangled with the overall study goal; these need to be disentangled
- 2) The objectives imply work on generalist arthropods whereas only 2 groups of these (spiders and ladybeetles) were examined; most of the other generalist predators in rice-field systems (ants, ground beetles, earwigs, crickets, predatory bugs) were not part of the study
- 3) No hypothesis is stated, and while this might not be absolutely necessary, it would be useful to add a small bit about what the study's expectations generally were, for the conclusions to be viewed by the general readership from the perspective of whether or not such expectations were met/achieved.

**[Reply]** We appreciate the reviewers for their time and effort. Please find our reply to each comment below. Line numbers in our reply refer to the revised version with tracked changes.

- 1) *Objectives and overall study goal* We have revised the last paragraph of our introduction to clarify our aim (Line 118), objectives (Line 122), and expectation (Line 127).
  
- 2) *Spiders and ladybeetles* a) We focused on these two groups (7 families) because they were the most abundant generalist arthropod predators (GAPs) in our study farms (Line 180). Other GAPs were rare or absent. For example, we did not find earwigs and ground beetles in our samples. b) We think that using spiders and ladybeetles to represent GAPs should be acceptable because it is common in the literature. Some examples are provided below:

#### *Spiders as GAPs*

Roubinet, E., et al. 2017. Diet of generalist predators reflects effects of cropping period and farming system on extra-and intraguild prey. *Ecological Applications*, 27(4): 1167-1177.

Suzuki, S.S., et al. 2023. Dynamics of species-rich predator-prey networks and seasonal alternations of core species. *Nature Ecology & Evolution*, 2023:1-12.

Ladybeetles as GAPS

Rana, J. S., et al. 2002. Costs and benefits of prey specialization in a generalist insect predator. *Journal of Animal Ecology*, 71.1: 15-22.

Thomine, Eva, et al. 2020. Highly diversified crop systems can promote the dispersal and foraging activity of the generalist predator *Harmonia axyridis*. *Entomol. Gen.*, 40.2 (2020): 133-145.

- 3) *Expectations* We appreciate this valuable suggestion and now include our expectations in the introduction (Line 127).
2. If applicable, is the application/theory/method/study reported in sufficient detail to allow for its replicability and/or reproducibility?

Please provide suggestions to the author(s) on how to improve the replicability/reproducibility of their study. Please number each suggestion so that the author(s) can more easily respond.

Reviewer #1: Mark as appropriate with an X:

Yes [X] No [] N/A []

Provide further comments here:

Reviewer #2: Mark as appropriate with an X:

Yes [] No [X] N/A []

Provide further comments here:

- 1) The sample sizes (number of farms) were unbalanced (3, 7 and 7 in the 1st, 2nd and 3rd years, respectively). There is need to clarify how the impact of this was addressed so as not to invalidate analyses methods applied
- 2) The sweep-netting strategy needs clarification (whether only ridge-side plants were swept, as the authors state, or a more representative method covering adequate sections of rice-field-plots were sampled). They speak of sweeping while walking along ridges
- 3) Need to add if field choice was randomized, and if so, how this was achieved for sampling independence
- 4) Sampling frequency not stated
- 5) 1-km buffer around farms to characterize forest cover effects on predation, is rather too far to have any impact on arthropod assemblages on the farms. the role of forest cover could well have been eliminated from the study

[Reply] Thank Reviewer 2 for pointing out these. Please see our reply below.

- 1) *Unbalanced sample size* To account for this issue, we now use weighted regression based on the number of observations from each year. Note that the new analysis (Table 1) does not change the conclusions of our study.
- 2) *Sweep-netting* As suggested, we now provide more details (Line 152): “At each major rice crop stage (seedling, tillering, flowering, and ripening stages) during the growing season (April - July) in each study year, we collected arthropod samples by sweep-netting (36 cm in diameter with a mesh size of 0.2 × 0.2 mm) the crop canopy 30 times in each of two transects inside a rice field. Each transect (ca 30 m long) was parallel to but 1.5m away from a randomly selected farm ridge.”
- 3) *Field choice* We have added more details to address this issue (Line 142): “We collected terrestrial arthropods in paired organic and conventional rice farms in subtropical Taiwan (120.656-120.721 °E; 24.364-24.489 °N) from 2017 to 2019 (three farm pairs in 2017 and seven farm pairs each in 2018 and 2019). While farms in the same pair were relatively close to each other (e.g., within a few hundred meters in distance), different farm pairs were at least 1 km apart from each other to reduce confounding effects. The study farms were 0.2 hectares on average and irrigated with surface water.”
- 4) *Sampling frequency* We collected samples at each major crop stage (seedling, tillering, flowering, and ripening stages) (Line 152), although the isotope data at the seedling stage were excluded from the analysis due to insufficient sample sizes for model estimation (Line 200).
- 5) *1-km buffer* Since there is no single standard for the buffer zone size, we followed the methods in previous studies. For example, Rusch et al. (2016) quantified landscape composition within a 1-km radius around the field and found a landscape effect on natural pest control. Karp et al. (2018) even used a 2-km radius to demonstrate landscape effects on crop pests and predators. To provide more information, we now cite Rusch et al. (2016) in the methods.

3. If applicable, are statistical analyses, controls, sampling mechanism, and statistical reporting (e.g., P-values, CIs, effect sizes) appropriate and well described?

Please clearly indicate if the manuscript requires additional peer review by a statistician. Kindly provide suggestions to the author(s) on how to improve the statistical analyses, controls, sampling mechanism, or statistical reporting. Please number each suggestion so that the author(s) can more easily respond.

Reviewer #1: Mark as appropriate with an X:

Yes  No  N/A

Provide further comments here:

Reviewer #2: Mark as appropriate with an X:

Yes  No  N/A

Provide further comments here:

- 1) Pest consumers were pooled at a taxonomic level rather too coarse (order) adequate isotopic signature resolution. Family level would have been much more acceptable

- 2) Mention is made of beta regression (GLM or GLMM) but not mention of probability distribution of link function employed in such modelling
- 3) Results of Isotopic analyses of food proportions in predators diets using MixSIAR should be presented in form of median with credible intervals rather than means and standard errors.

**[Reply]**

- 1) *Taxonomic level* Please see our reply to Editor's comments above (*Arthropods were pooled*).
- 2) *Probability distribution* As suggested, we now add more details in our methods (Line 210): “To examine how local abiotic and biotic factors may affect the pest consumption by GAPs, we fit generalized linear models (GLMs) with a beta distribution and a logit link function using the R betareg package (Zeileis *et al.*, 2016), with year, farm type, crop stage, percent forest cover, and the relative abundance of rice herbivores as fixed effects and the proportion of rice herbivores consumed in predators’ diet as the response variable (i.e., posterior medians from the Bayesian stable isotope mixing models).”
- 3) *Medians vs. means* Thank Reviewer 2 for this constructive comment. As suggested, we have updated our analysis using posterior median estimates. We also update related tables (Table 2 and 3) and figures (Fig. 1 and 2). Compared to our previous analysis, the new one generates a quantitative but not qualitative change in the results. Therefore, the new analysis does not alter the conclusions of our study.
4. Could the manuscript benefit from additional tables or figures, or from improving or removing (some of the) existing ones?

Please provide specific suggestions for improvements, removals, or additions of figures or tables. Please number each suggestion so that author(s) can more easily respond.

Reviewer #1: No

Reviewer #2:

- 1) There should be at least one table summarizing median and credible intervals of pest proportions in predator diets.
- 2) Figures from the MixSIAR results should presented in form of posterior density plots of medians, not linear graphs of means.
- 3) Therefore tables and figures presenting results in form of means and standard errors should be removed.

**[Reply]**

- 1) *Summary table* We have updated our Table 2 and 3 accordingly. Please see our reply to Reviewer 2’s comments on Results below (*Report the medians*) for how we calculate the means of the posterior medians from Bayesian stable isotope mixing models.
- 2) *Figures from the MixSIAR* Please see our reply to Reviewer 2’s comments on Results below (*Report the medians*) to clarify this issue.

- 3) *Means and standard errors* Please see our reply to Reviewer 2's comments on Results below (*Report the medians*) to clarify this issue.

5. If applicable, are the interpretation of results and study conclusions supported by the data?

Please provide suggestions (if needed) to the author(s) on how to improve, tone down, or expand the study interpretations/conclusions. Please number each suggestion so that the author(s) can more easily respond.

Reviewer #1: Mark as appropriate with an X:

Yes  No  N/A

Provide further comments here:

Reviewer #2: Mark as appropriate with an X:

Yes  No  N/A

Provide further comments here:

- 1) The results as currently presented are based on means and standard errors of MixSIAR models. These carry a high level of inaccuracy because MixSIAR model estimates of food source proportions are typically skewed, making means very vulnerable to effects of statistical tails. Medians are the most resilient to such impacts, but include credible intervals
- 2) The authors state that generalist predators qualify as specialists because they have high proportions of pest food in their diets towards crop maturity, without providing justifiable evidence
- 3) Throughout the article, there is need to emphasize that the study was based on two groups of generalist predators only - (spiders and ladybeetles), and not make an overarching generalization for all generalist predators

[Reply]

- 1) *Medians* As suggested, we have updated our analysis using posterior median estimates. Please see our reply to Reviewer 2's comments on Results below (*Report the medians*) for more details.
- 2) *Generalist predators qualify as specialists* Thanks for raising this issue. First, it seems that the reviewer may define specialists at the species level, but this study focuses on the feeding-guild level (e.g., rice herbivores). To clarify this, we now use “guild-level specialist predators” or “predators function as pest specialists” in our article (Line 309, 315, 322, and 435). Second, this study shows that these generalist predators consumed a high proportion of rice pests in their diets (e.g., 80-97%) at late crop stages. Therefore, we suggest that these predators function as guild-level specialists (Line 29-33, 296-300, and 320-327).
- 3) *Generalization* We understand this concern and have clarified this issue by using “spiders and ladybeetles” (Line 250) or “both predators” (Line 255, 271, 277, 285, and 288) instead of “all predators”. Regarding the representation and meaning of these predators, please see our reply to Reviewers’ comment 1 above (*Spiders and ladybeetles*).

6. Have the authors clearly emphasized the strengths of their study/theory/methods/argument?

Please provide suggestions to the author(s) on how to better emphasize the strengths of their study. Please number each suggestion so that the author(s) can more easily respond.

Reviewer #1: Yes

Reviewer #2: In general yes

**[Reply]** We thank both reviewers for their positive comments.

7. Have the authors clearly stated the limitations of their study/theory/methods/argument?

Please list the limitations that the author(s) need to add or emphasize. Please number each limitation so that author(s) can more easily respond.

Reviewer #1: No

Reviewer #2: In the limitations/caveats subsection, the authors state that they are reluctant to imply actual pest suppression because they did not complement isotopic analyses (SIA) with direct field observation. The SIA technique is meant to more or less eliminate the need for direct field observation, or at least render it subliminal. Here its better to say that the study did not incorporate assessment of crop damage rates or yield gap data to support implications of pest suppression

**[Reply]** As suggested, we now add this sentence to the section that addresses study limitations (4.4. *Potential caveats of this study*): “Furthermore, future work may examine crop damage and production to reveal the effect of GAPs on pest control and crop performance.” (Line 418).

8. Does the manuscript structure, flow or writing need improving (e.g., the addition of subheadings, shortening of text, reorganization of sections, or moving details from one section to another)?

Please provide suggestions to the author(s) on how to improve the manuscript structure and flow. Please number each suggestion so that author(s) can more easily respond.

Reviewer #1: Yes

Reviewer #2: Generally no, except for the need to clearly dis-engage or distinguish the study's mail aim/goal from objectives and hypothesis, putting all these in a stand-alone paragraph under Introduction section

**[Reply]** We appreciate this suggestion. Our introduction has been revised to clarify the aim (Line 118), objectives (Line 122), and expectation (Line 127) of this study.

9. Could the manuscript benefit from language editing?

Reviewer #1: No

Reviewer #2: No

**[Reply]** Thank both reviewers for the positive feedback.

## Reviewer 1's comments

In this paper the authors investigated the role of generalist and specialist predators in the rice ecosystem. They employed stable isotope approach to test three hypotheses. They found predation on pests increased over season, was similar across years, and was higher in conventional than organic farming. They conclude that generalist predators have potential to produce stable top-down effect. The study investigates an important topic, the design was adequate and the results are sound but not in current version.

I have two major concerns. At first, the role of generalist spider predators has been known for a long time. So in this respect the study does not bring anything novel. But the quantification of rice pest suppression is new. Yet, this is the main problem of the study. The isotopic analysis is not the best to be used to quantify trophic interactions as it lacks the precision. In particular, the absence of intraguild predation is intriguing. The estimates of predation on pests are thus biased to an unknown degree. This is a serious limit of the study. Unfortunately, the authors acknowledge this limit only in the very last part of Discussion, so the reader is impressed by reading the paper how efficient spiders are in pest suppression. The authors should either provide evidence that intraguild prey was scarce and therefore unlikely to form a significant proportion of the diet or state this limit in the beginning of the study.

In addition I find both Introduction and Discussion excessively long. For example, the first paragraph of Introduction could be omitted as it is too general.

**[Reply]** We thank these comments and address the two main concerns raised by Reviewer 1 below.

- 1) *Limitations of this study* a) We agree with the reviewer that stable isotope analysis may not be as precise as other methods (e.g., molecular analysis of gut contents), but it has an advantage in reflecting accumulated prey consumption in predators' diets (Line 135). This time-integrated diet information can be valuable to agroecologists. b) Stable isotope analysis has been developed rapidly in the past two decades and increasingly applied in ecological studies (Quinby et al. 2020), especially in the field of predator-prey trophic interactions (Blumenthal et al. 2012, Manlick et al. 2019, Carbonell Ellgutter et al. 2020). This study will add to the existing body of knowledge as it can provide predators' diet composition over crop stages, farm types, and years. c) That being said, we appreciate the reviewer comment and therefore now mention "the potential caveats of this study (e.g., pest suppression and intraguild predation)" earlier in this article (Line 311).

#### References:

- Quinby, B. M., Creighton, J. C., & Flaherty, E. A. (2020). Stable isotope ecology in insects: a review. *Ecological Entomology*, 45(6), 1231-1246.
- Blumenthal, S. A., Chritz, K. L., Rothman, J. M., & Cerling, T. E. (2012). Detecting intraannual dietary variability in wild mountain gorillas by stable isotope analysis of feces. *Proceedings of the National Academy of Sciences*, 109(52), 21277-21282.
- Manlick, P. J., Petersen, S. M., Moriarty, K. M., & Pauli, J. N. (2019). Stable isotopes reveal limited Eltonian niche conservatism across carnivore populations. *Functional Ecology*, 33(2), 335-345.

Carbonell Ellgutter, J. A., Ehrich, D., Killengreen, S. T., Ims, R. A., & Unnsteinsdóttir, E. R. (2020). Dietary variation in Icelandic arctic fox (*Vulpes lagopus*) over a period of 30 years assessed through stable isotopes. *Oecologia*, 192, 403-414.

- 2) *Intraguild predation* Please see our reply to Editor's comments above (*The lack of intraguild predation*).
- 3) *Long introduction and discussion* We have shortened the two sections accordingly. Please see our reply to Editor's comments (*Long introduction and discussion*).

Line 18: Rather than biocontrol use Conservation control.

**[Reply]** We thank this suggestion. Since conservation biological control is only a subfield of biocontrol and may not include all the practices (e.g., supplemental release of natural enemies), it might be better to keep the original wording (biocontrol) here.

Lines 86-90: To test the hypothesis of consistency is trivial unless there is a reason why generalists as opportunists would switch to a different prey some years.

**[Reply]** Arthropod densities and compositions often fluctuate over years in agroecosystems (Line 89). Accordingly, generalist arthropod predators (GAPs) with an opportunistic feeding strategy may change their diet composition. Therefore, examining the consistency of GAPs in pest consumption over years is important to evaluate GAPs' role as biocontrol agents.

Lines 125-128: Repetition of the former text. Omit it.

**[Reply]** We have revised this paragraph to remove repetition and clarify our aim (Line 118), objectives (Line 122), and expectation (Line 127).

Line 145: I am surprised to read that the conventional farms used only one application of insecticide per season. Is it really true?

**[Reply]** Yes, only one application per season was reported from our study farms. Note that pesticide application also increases the cost of farming (operating on low margins). If farmers grow rice in late summer (not in this study), two applications of pesticides might be conducted due to high pest density.

Lines 143, 145: Add information when the insecticides were applied.

**[Reply]** As suggested, we now add this information (Line 150, 152).

Line 147: How often sweeping was done? Once per growing stage?

**[Reply]** Yes, we collected samples by sweep-netting once at each crop stage (Line 152).

Line 150: To what taxonomic level identification was performed? And how was it identified?

**[Reply]** We identified common arthropods to species level and less common ones to genus or family level. We now add the taxonomic level to our article (Line 159). Species identification was based on insect pest handbooks in Taiwan and Southeast Asia or experts' assessment from the Department of Entomology at our university.

Line 159: I wonder why there were only 352 predators but 828 prey samples if the study plots were dominated by a single pest species?

**[Reply]** 1) These samples were replicates from different farms, crop stages, and years. Different samples could consist of the same species, and therefore sample numbers may not reflect much information about species numbers. 2) Yes, major rice herbivores in our study farms included a few species of planthoppers, leafhoppers, and stink bugs (Line 181). 3) Our predators consumed at least three prey guilds (rice herbivores, tourist herbivores, and detritivores). Therefore, this study had more prey samples than predator samples for isotope analysis.

Lines 167-170: Omit definition of guilds.

**[Reply]** Since some readers are less familiar with the concept of trophic guilds, which play a critical role in our analysis, we hope to keep this short explanation here.

Line 189: If samples at seedling stage were later omitted why do you earlier say that you collected data at four growing stages?

**[Reply]** 1) Thanks for asking this question. While we collected data from four stages, seedling stage was omitted from our stable isotope analysis due to insufficient sample size for model estimation (Line 200). 2) However, this was not an issue for other analyses. For example, seedling stage was included in the analysis of relative prey abundance (Fig. 3).

Line 203: How did you estimate the proportion of herbivores? This must have been done by the model. Explain.

**[Reply]** The analyses includes two parts. First, we ran Bayesian stable isotope mixing models to estimate the proportion of different sources (i.e., rice herbivores, tourist herbivores, and detritivores) in predators' diet (Line 193). Next, we extracted the posterior median estimates of rice herbivore consumption from the Bayesian stable isotope mixing models and fit GLM models to examine how this consumption may be affected by local abiotic and biotic factors (Line 210).

Lines 264-267: This belongs to Discussion.

**[Reply]** As suggested, we have removed this sentence from the Results.

Lines 269-270: I am surprised to read the absence of association between proportion of herbivores in the predator body and their abundance in the field. If spiders are generalists then there should be such association. This makes the obtained results suspicious.

**[Reply]** 1) Yes, we were surprised as well, especially when there seemed to be a positive correlation between the rice herbivore consumption by predators (Fig. 1) and the relative abundance of rice herbivores in the field (Fig. 3). 2) However, the relative abundance of rice herbivores in the field also increased with crop stages. When all factors were included in our GLM models, most variations were explained by crop stage (significant) but not the relative abundance of rice herbivores (non-significant). 3) This explanation is provided in Discussion (Line 400).

Lines 274-294: This is just repetition of results. Omit it.

**[Reply]** Since this study investigated multiple topics and reported relatively rich information in Results, we think a brief summary and synthesis here will help our readers orient themselves.

Lines 331-344: This is trivial. Omit it.

**[Reply]** Examining the consistency of generalist predators in pest consumption over years will provide critical information to biocontrol programs (Line 86), but relevant information is lacking (knowledge gap 2 highlighted in this study). Given that our results suggest that these predators can be a consistent tool for pest management under various environmental conditions, we think we should briefly address this important finding in Discussion.

Lines 357-367: This is trivial. Omit it.

**[Reply]** This paragraph briefly discusses the effect of crop stage (a statistically significant factor in this study) on pest consumption and provides a suggestion for pest biocontrol. This paragraph should provide valuable insights for agricultural practices, and therefore we hope to keep it. That being said, we have shortened this paragraph.

## Reviewer 2's comments

The study examined rates of consumption of a range of arthropod herbivores (pests) in rice-fields of Taiwan by spiders and lady beetles, by using stable isotopes mixing models MixSIAR to estimate proportional contributions of these pests to predators' diets. They additionally evaluated the influence of some habitat variables in contributing to such pest consumption trends, comparing organic versus conventional farming systems over three consecutive years.

This is a very significant study, with potential to contribute immensely to the still narrow range of literature on the general subject of new techniques and strategies for quantifying pest biocontrol in cereal crops. It is also very timely, given the increasing value attachment to non-chemical measures for mitigating crop damage by arthropod pests. The element of crop growth stage as a factor in determining pest consumption levels is especially interesting as it is rarely examined yet arthropod assemblage patterns, and presumably their trophic interactions do change with time.

While the study is generally well designed, it has a number of methodological gaps that would need to be addressed so as to put the results into proper perspective for conclusions to be justifiably drawn. These include wide generalizations about the range of predators examined

(while only two taxonomic groups were involved), and combining pest consumers at taxonomic levels too course for isotopic analyses. Habitat variables' roles and how they were characterised are also not adequately described while samples (farm numbers) were not consistently balanced to justify temporal-scale comparisons. In addition, results of MixSIAR modelling that form the basis of the discussion and conclusions drawn are presented in form of means and standard errors while the conventional practice is to present medians and credible intervals. There are some inconsistencies (or gaps) in some non-MixSIAR analyses of data, particularly with regression, and a few non-clarifications on the study's objectives.

**[Reply]** We appreciate the positive and constructive comments from the reviewer. We agree with the reviewer that this is a significant and timely study in agroecology. Below we address the main concerns raised by the reviewer.

- 1) *Two taxonomic groups of predators* This study focused on spiders and ladybeetles because they were the most abundant GAPs in our study farms. Please see our reply to Reviewers' comment 1 above (*Spiders and ladybeetles*) for more detailed explanation. To clarify this issue, we now use "spiders and ladybeetles" (Line 250) or "both predators" (Line 255, 271, 277, 285, and 288) instead of "all predators".
- 2) *Combining pest consumers* The diet composition of this study focused on trophic guilds, and therefore arthropods were grouped into a particular guild if they used similar resources. The grouping was based on a combination of literature surveys and k-means clustering of carbon and nitrogen isotope signatures of arthropod samples (Line 185). Please see more details in our reply to Editor's comments above (*Arthropods were pooled*).
- 3) *Habitat variables* To clarify the variables in our data analysis, we have refined the last paragraph of Introduction (Line 210): "To examine how local abiotic and biotic factors may affect the pest consumption by GAPs, we fit generalized linear models (GLMs) with a beta distribution and a logit link function using the R betareg package (Zeileis *et al.*, 2016), with year, farm type, crop stage, percent forest cover, and the relative abundance of rice herbivores as fixed effects and the proportion of rice herbivores consumed in predators' diet as the response variable..."
- 4) *Unbalanced farm numbers* Thank the reviewer for raising this issue. To solve this issue, we have updated our analysis using weighted regression based on the number of observations in each study year. Note that the new analysis (Table 1) does not change the conclusions of our study.
- 5) *Means vs. medians* Thanks for this constructive comment. As suggested, we now use posterior median estimates and update related tables (Table 2 and 3) and figures (Fig. 1 and 2). Note that this new analysis generates a quantitative but not qualitative change in our results. Therefore, our conclusions remain unchanged.
- 6) *Inconsistencies in regression* We have clarified the confusions. Please see details in our reply to each specific question Reviewer 2 had for the Methods section (below).

- 7) *Study objectives* As suggested, we have clarified the aim (Line 118), objectives (Line 122), and expectation (Line 127) of this study.

Title:

The current title implies that all generalist predators were studied, which is not the case - only spiders and lady beetles were considered. Suggested change: Spiders and lady-beetles consume higher proportions of rice pests at late growth stages regardless of farming system. This is because there were only 2 predator groups examined here: spiders and lady beetles

**[Reply]** a) Our stable isotope analysis focused on the most abundant generalist arthropod predators (GAPs) in rice paddies, which happened to be spiders and ladybeetles (7 families in total) across three years of study (Line 180; Table S1). b) We understand the reviewer's concern and have clarified this issue by using "spiders and ladybeetles" (Line 250) or "both predators" (Line 255, 271, 277, 285, and 288) instead of "all predators". c) Spiders and ladybeetles consume a wide range of preys and are typical generalist arthropod predators (GAPs). Therefore, they are often used to represent generalist predators in literature. Some examples from a long list are provided below. d) All together, we think that we now provide a clear definition of GAPs, and it should be acceptable to use this term in this study.

Spiders as GAPs

Roubinet, E., et al. 2017. Diet of generalist predators reflects effects of cropping period and farming system on extra-and intraguild prey. *Ecological Applications* 27(4): 1167-1177.

Suzuki, S.S., et al. 2023. Dynamics of species-rich predator-prey networks and seasonal alternations of core species. *Nature Ecology & Evolution* 2023:1-12.

Ladybeetles as GAPs

Rana, J. S., et al. 2002. Costs and benefits of prey specialization in a generalist insect predator. *Journal of Animal Ecology* 71.1: 15-22.

Thomine, Eva, et al. 2020. Highly diversified crop systems can promote the dispersal and foraging activity of the generalist predator *Harmonia axyridis*. *Entomol. Gen.* 40.2 (2020): 133-145.

Abstract

1. This is generally well summarised, but elements of it and some wordings/sentences will change after some of the results-presentation suggestions are addressed.
2. Also the claim of predators being specialist towards crop maturity is unsupported by the results

**[Reply]**

- 1) *Generally well summarized* We appreciate this positive comment and have updated the abstract accordingly. Please note that the new updates do not change the conclusions of our study.
- 2) *Predators being specialist* It seems that our reviewer may define specialists at the species level, but our study focuses on the feeding-guild level (e.g., rice herbivores). We have

clarified this issue and modified the manuscript accordingly. Please see details in our reply to Reviewers' comment 5 above (*Generalist predators qualify as specialists*).

#### Introduction

1. The objectives stated but are entangled with the overall study goal; these need to be disentangled
2. The objectives imply work on generalist arthropods whereas only 2 groups of these (spiders and ladybeetles) were examined; most of the other generalist predators in rice-field systems (ants, ground beetles, earwigs, crickets, predatory bugs) were not part of the study
3. No hypothesis is stated, and while this might not be absolutely necessary, it would be useful to add a small bit about what the study's expectations generally were, for the conclusions to be viewed by the general readership from the perspective of whether or not such expectations were met/achieved
4. The role of 'years', in my opinion would not make a significant value since the rice agronomic practices do not change much from year to year in the study area (Taiwan). Therefore the crop stages are enough as a time-based parameter.
5. There is need to clearly distinguish amongst: overall goal/aim(s); specific objectives; the study's expectations or working hypotheses. As at now, they seem to be all mixed up towards the end of the introduction section

#### [Reply]

- 1) *Objectives* We have revised the last paragraph of our introduction to clarify our aim (Line 118), objectives (Line 122), and expectation (Line 127).
- 2) *Spiders and ladybeetles* We have clarified this concern in our reply to Reviewer 2's comment on Title (above).
- 3) *Hypothesis or expectation* As suggested, we have revised our introduction to clarify our aim (Line 118), objectives (Line 122), and expectation (Line 127).
- 4) *The role of years* We understand the reviewer's point. However, the climate may differ a lot over years (e.g., Fig. S3 for this study), leading to a change in prey composition (e.g., Table S3 for this study). Therefore, examining GAPs' consistency in pest consumption over years becomes a meaningful topic in pest management.
- 5) *Aim, objectives, and expectations* As suggested, we have clarified our aim (Line 118), objectives (Line 122), and expectation (Line 127).

#### Methods

1. Three farms in year one and 7 farms each in year 2 and 3 amounts to unbalanced sample size
2. The authors need to more fully and clearly describe how mist-netting was conducted: it's not enough to say this was conducted while walking along ridges, because this implies sampling only insects along field edges, rendering the collected samples un-representative
3. Sweeping for canopy insects also implies that insects on other aerial parts of rice were ignored: not all pests are to be found on rice canopies (under-representation or under-sampling)

4. Also how plots were selected for sampling including distance separation between sampled plots, and how this was independent of arthropod movement patterns (to eliminate pseudoreplication) will be desirable
5. It would have been useful if the study assessed the role of some surrounding vegetation on field margins (eg on ridges and levees) as a food source alternative to rice, and how it compares to rice as a contributor to pest diets. This is because It could be that the reason predators consume more rice prey in late stages is that at this time, drier conditions and no water support little growth of alternative plants such as on ridges and levees, making herbivores move from there and be more abundant in rice. Consequently, predator-prey interactions are enhanced on rice, in which case the key explanatory factor here is therefore the watering regime rather than the crop stage. In the absence of this data/results, the authors need to adequately describe the structure of this kind of vegetation, including its persistence across the grow-out period and water availability, for there to be a clear picture as to why it might not have affected predator or pest dispersal or consumption rate results presented
6. The role of habitat variables in driving predation rates has been treated very subliminally: not included in the objectives, not thoroughly described in Methods as to how the habitat structure (forest cover, other vegetation on field margins etc) were measured. Mention is made of forest cover, but no details as to how this was measured either, other that GoogleEarth was used for estimates. How close within the 1-km buffer were the forests to the rice-fields, for there to be an expectation that arthropods they might influence predation rates on farms? A 1-km buffer around farms is quite wide and though a few mobile arthropods may disperse from there into farms (certainly not spiders and lady-beetles!!!), it will definitely not affect pest-predator trophic interactions

**[Reply]**

- 1) *Unbalanced sample size* To account for the unbalanced design, we have updated our GLM beta regression by using weights based on the number of observations in each study year. Note that the new analysis (Table 1) does not change the conclusions of our study.
- 2) *Sweep-netting* As suggested, we now provide more complete sampling methods (Line 152). Please see details in our reply to Reviewers' comment 2 above (*Sweep-netting*).
- 3) *Sweeping for canopy insects only* a) We understand this concern. Rice plants at late stages were too dense to conduct under-canopy sweeping. Therefore, we swept the upper half of vegetation. b) The samples we collected include most rice arthropod species reported from the literature. Therefore, our sampling method seems to be reasonable. One explanation is that most species inhabit both lower and upper halves of rice plants. Therefore, our method can catch these species. Even if a small number of species prefer to stay in the lower half of vegetation, they may be disturbed by sweeping-netting and therefore caught by us.
- 4) *Plots for sampling* We now add detailed information in Methods (Line 142): "We collected terrestrial arthropods in paired organic and conventional rice farms in subtropical Taiwan (120.656-120.721 °E; 24.364-24.489 °N) from 2017 to 2019 (three farm pairs in 2017 and seven farm pairs each in 2018 and 2019). While farms in the same pair were relatively close

to each other (e.g., within a few hundred meters in distance), different farm pairs were at least 1 km apart from each other to reduce confounding effects...”.

- 5) *Surrounding vegetation on rice farm ridges* a) Thank the reviewer for asking this question. Although we did not quantify plant communities on farm ridges, ridge vegetation remained green over the whole rice season. Therefore, it is less likely that herbivores on ridges need to move away to find new host plants. b) Plants on ridges usually include *Biden pilosa* and Poaceae weeds, which are not the main host plants for our rice herbivores (e.g., brown planthopper). Also, ridges are usually narrow (<1m wide) and support limited plant biomass due to farm management. Therefore, ridge vegetation may only play a minor role in our study. c) Water level in rice farms is less likely to explain our results (e.g., increasing herbivore density towards late crop stages). This is because water level is generally high at seedling and flowering stages (to suppress weeds and increase yield, respectively), but low at tillering and ripening stages (to increase deep roots and facilitate harvesting, respectively), inconsistent with observed high herbivore density at both flowering and ripening stages. d) Since both editor and Reviewer 1 asked us to shorten the discussion section, we will not add this reply (*Surrounding vegetation on rice farm ridges*) to our discussion.
- 6) *The role of habitat variables* a) As suggested, we now clarify the variables in our data analysis (Line 210): “To examine how local abiotic and biotic factors may affect the pest consumption by GAPs, we fit generalized linear models (GLM) with a beta distribution and a logit link function using the R betareg package (Zeileis et al., 2016), with year, farm type, crop stage, percent forest cover, and the relative abundance of rice herbivores as fixed effects and the proportion of rice herbivores consumed in predators’ diet as the response variable...”. b) Regarding the percent forest cover, there is no single standard for buffer zone, and therefore we follow the methods from previous studies. Please see details in our reply to Reviewers’ comment 2 above (*1-km buffer*).

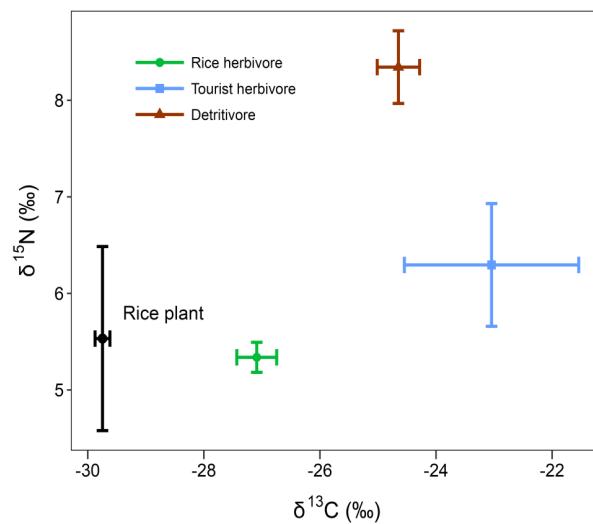
#### Analysis

1. Combining/pooling pest consumers at order level seems very coarse for isotopic signature resolution. In stable isotopic analyses, pooling up consumers' food sources into similar guilds is usually a generally acceptable and realistic strategy which helps in saving time, effort and costs without risk of losing signature resolution for food source signatures in predators, for instance. However, this should usually be done at as low a taxonomic level as possible, say genus or family. Pooling food sources at order level seems like a rather wide stretch, not least because at that level, despite guild-commonality, feeding systems are so variant as to erode isotopic signature resolution roles of component groups in contributing to consumer diets. In your case, grouping grasshoppers with beetles is rather strange, especially as you said earlier that former has no trophic link to rice. Putting hemiptera and lepidoptera is equally awkward since some hemiptera are generalist predators or omnivores. Finally, omitting crickets as part of detritivores is curious
2. Mention is made of beta regression but not probability distribution or link function applied, or whether this was conducted using GLM or GLMM modelling
3. ANOVA procedure is stated to have been applied to analyse some data that were supposedly analysed using beta regression. Why would such repetition be necessary?

4. From the unbalanced sample size 3, 7 and 7 farms) across the three years, assessment of the role of years would have requires a statement as to how such imbalance was addressed before analyses were performed in beta regression, eg incorporating a Kenward-Roger approximation with an autoregressive data structure, so as to reduce the impact of data heterokedascity
5. It is also not clear whether the interactive influences of the various explanatory factors were performed on mean, medial or other values of food-source proportions from MixSIAR, of from other datasets. This should be clarified

### [Reply]

- 1) *Combining/pooling pest consumers* a) While we identified arthropods to the lowest possible taxonomic level, we grouped them into different trophic guilds based on their food sources. Please see our detailed reasoning in the reply to Editor's comments above (*Arthropods were pooled*). b) Our grouping method should be reasonable because it is based on a combination of literature surveys and k-means clustering of carbon and nitrogen isotope signatures of arthropod samples (Line 185). Furthermore, we now provide a stable isotope biplot to demonstrate the differences among prey sources (Appendix A: Fig. S1). The small variation in rice herbivores (Fig. S1 below) indicates a common food resource (rice plants) for this group, supporting our grouping method. In summary, while these rice herbivores are from different taxa, they basically use rice as their main host plant. c) We understand the reviewer's concern for different arthropod taxa. Regarding Hemiptera, we found herbivory species (common) and predatory species (rare) in rice farms and only included the herbivory ones in our analysis (rice herbivore guild). Regarding grasshoppers and leaf beetles, they primarily fed on ridge vegetation but not rice plants, and therefore were grouped into the tourist herbivore guild. Regarding crickets, they were rare in our samples (likely due to irrigation) and therefore not included in our analysis.



**Figure S1.** Stable isotope biplot of the rice plant and three prey sources in this study. Error bars represent 95% confidence intervals.

- 2) *GLM details* As suggested, we now add more details in our methods (Line 210): “To examine how local abiotic and biotic factors may affect the pest consumption by GAPs, we fit generalized linear models (GLM) with a beta distribution and a logit link function using the R betareg package (Zeileis *et al.*, 2016)...”.
- 3) *ANOVA procedure* The “Anova” function (Line 221) was applied to the GLM beta regressions to assess the significance of each factor in the model using the likelihood ratio test. It was not used to perform the analysis of variance (not to be confused with the function name).
- 4) *Unbalanced design* As suggested, we have updated our analysis using weighted regression based on the number of observations in each study year. Note that the new analysis (Table 1) does not change the conclusions of our study.
- 5) *Clarify explanatory and response variables* We now clarify variables in our analysis (Line 210): “To examine how local abiotic and biotic factors may affect the pest consumption by GAPs, we fit generalized linear models (GLM) with a beta distribution and a logit link function using the R betareg package (Zeileis *et al.*, 2016), with year, farm type, crop stage, percent forest cover, and the relative abundance of rice herbivores as fixed effects and the proportion of rice herbivores consumed in predators’ diet as the response variable (i.e., posterior medians from the Bayesian stable isotope mixing models)...”.

## Results

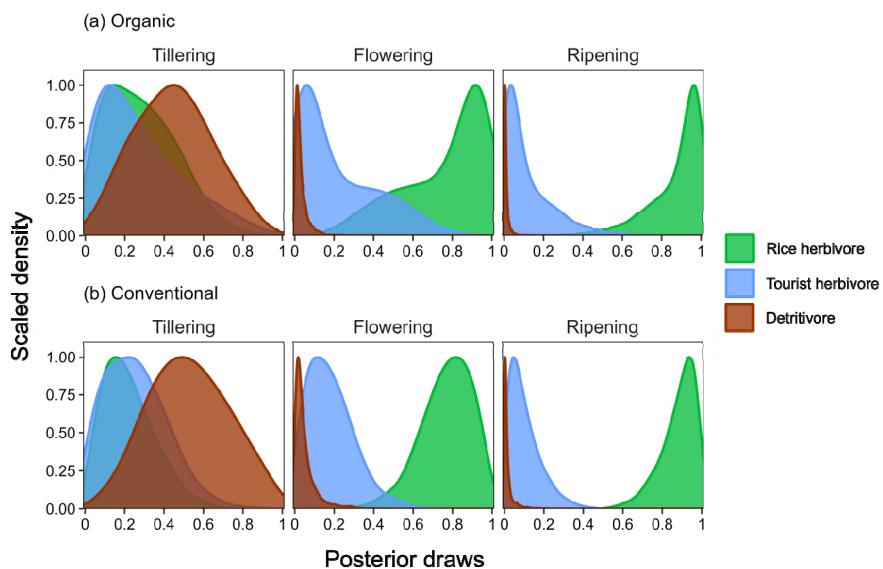
1. The results of the isotopic mixing models for pest contributions to predator diets should be presented in form of Medians accompanied corresponding by credible intervals, instead of Means and standard errors as the authors have done. This is because normally, the mean is more relevant when aspiring for a definite hypothesis test with normally-distributed (or transformed data) to reduce skewing and so we can test to get a p-value 0.05 etc) because mean is very sensitive or vulnerable to errors arising from long statistical-distribution tails. By contrast, with the Bayesian MixSIAR modelling, food proportion estimates, are almost always skewed so a measure of means is even more vulnerable to such impacts of tails (skewing), and the better option is therefore to use the median, which has the least sensitivity to skewed tails (compared to means or modes). But one has to provide the credible intervals to accompany the medians, just as you need SD (not just SE as the authors have done here) to accompany means in direct hypothesis tests. Therefore, the authors need to go back to their MixSIAR model results isotopic results and construct results based on medians. For details on this, see various articles by Brian Stock and Semmens.
2. The results of the medians should consequently be presented in at least 1 table, and also the figures should preferably be presented in form of posterior median density plots (usually generated automatically by MixSIAR) rather than the linear graphs presented here by the authors
3. After that results change, the patterns and trends in food source contributions to consumer diets will change a lot, the authors will need to re-write results section
4. There is not justifiable case for implying that because proportions of pests in generalist predators diets are relatively higher towards crop maturity, these predators then become

specialists. You would have to quantify each of the component herbivores individually to see if they are consuming only one type at that stage (diet specialization/monophagy)

5. The role of habitat variables in driving predation rates have not been clearly treated in results, so it is not easy to see how they influenced observed predation patterns. They could well be eliminated from the paper

### [Reply]

- 1) *Use medians* As suggested, we now use posterior median estimates and update related tables (Table 2 and 3) and figures (Fig. 1 and 2). Note that this new analysis generates a quantitative but not qualitative change in our results. Therefore, our conclusions remain unchanged.
- 2) *Report the medians* a) Thanks for this suggestion. Please note that we now report the means of the posterior medians from Bayesian stable isotope mixing models in Table 2-3 and Fig. 1-2. b) Let us clarify our analysis here. First, we ran Bayesian stable isotope mixing models to estimate the proportion of different prey sources (i.e., rice herbivores, tourist herbivores, and detritivores) in predators' diet (Line 193). The models would return a posterior distribution for each prey source at each crop stage in each individual farm in each study year. Next, as suggested by the reviewer, we extracted the posterior median estimates of rice herbivore consumption from the Bayesian stable isotope mixing models (Line 208) and fit GLM models to examine how this consumption may be affected by local abiotic and biotic factors (Line 210). c) We have a lot of replicates and more than a hundred of posterior density plots. Therefore, it is unlikely to report all of these plots. Also, it should be unnecessary since the means of the posterior medians have been reported in Table 2-3 and Fig. 1-2. That being said, we provide one example below to show the posterior distribution for one of the study farm pairs in 2017.



- 3) *Re-write the results* As we explained above, using medians (suggested by the reviewer) instead of means (analyzed in our previous version) does not generate qualitative changes. We have updated the numbers reported, but our conclusions remain the same.
- 4) *Diet specialization* Thank Reviewer 2 for mentioning this. Yes, predators in our study may still consume a few rice herbivore species at late crop stages and therefore should be considered as “generalists” by definition. What we would like to highlight here is that these predators mainly consumed rice herbivores at late crop stages (80-97% in predators’ diets) and therefore functioned as specialists of rice herbivores (i.e., guild-level but not species-level specialist). To clarify this, we now use “guild-level specialist predators” or “predators function as pest specialists” in our article (Line 309, 315, 322, and 435).
- 5) *Habitat variables* A few abiotic and biotic variables have a potential to influence the biocontrol effect of generalist predators and have been examined in previous studies (Line 93). Related findings will provide insights for agricultural management (Line 116). Therefore, we hope to keep this part of results (*Results 3.3. Factors associated with rice herbivore consumption by predators*; Line 269).

#### Discussion

1. I have largely hesitated to review this section due to the changes that will likely result from the presentation of results of Median instead of Mean proportional contributions of pests to predator diets because after that results change, the patterns and trends in food source contributions to consumer diets will change a lot, the authors will need to re-write discussion and conclusion sections

**[Reply]** As mentioned above, the new analysis (using medians instead of means) does not change the conclusions of our study. We now make our discussion more concise, as suggested by editor and Reviewer 1. Overall, this manuscript has been improved following the comments of editor and reviewers.

1    *Submission type: Research article*

2

3    **A predator in need is a predator indeed: generalist arthropod predators**  
4    **function as pest specialists at the late growth stage of rice**

5

6    Gen-Chang Hsu<sup>1</sup>, Jia-Ang Ou<sup>2,3</sup>, Min-Hsuan Ni<sup>2</sup>, Zheng-Hong Lin<sup>2</sup> and Chuan-Kai Ho<sup>1,2\*</sup>

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17

## Abstract

18 Biocontrol, using natural enemies for pest control, has a long history in agriculture. It has  
19 received a surge of interest in the recent Anthropocene because of its potential as a valuable tool  
20 for sustainable agriculture. To solve a long-standing puzzle in biocontrol—how well the  
21 ubiquitous generalist arthropod predators (GAPs) function as biocontrol agents—this study  
22 aimed to 1) quantify the diet composition of GAPs at each crop stage using stable isotope  
23 analysis, 2) examine the consistency of GAPs in pest consumption over years, and 3) investigate  
24 how abiotic and biotic factors affect pest consumption by GAPs~~the diet composition of these~~  
25 ~~predators~~. Specifically, we sampled arthropod prey and GAPs in sub-tropical organic and  
26 conventional rice farms over crop stages (seedling, tillering, flowering, and ripening) in three  
27 consecutive years. Among our field-collected samples, 352 arthropod predator and 828 prey  
28 isotope samples were analyzed to infer predator-prey interactions. Our results show the  
29 following: a) The proportion of rice pests in GAPs' diets in both organic and conventional farms  
30 increased over the crop season, from 2~~13~~-47% at the tillering stage to 80~~79~~-97~~5~~% at the ripening  
31 stage, across the three study years. The high percentage in pest consumption at late crop stages  
32 (flowering and ripening) suggests that GAPs can function as specialists in pest management  
33 during the critical period of crop production. Regarding individual predator groups, spiders and  
34 ladybeetles exhibited distinct dietary patterns over crop stages. b) The high pest consumption by  
35 GAPs at late crop stages was similar across years (with different climatic conditions), suggesting  
36 a consistency in GAP feeding habits and biocontrol value. c) The proportion of rice pests in  
37 GAPs' diets varied with farm type and crop stage (e.g., higher in conventional farms and during  
38 flowering/ripening stages). By quantifying the diet composition of GAPs over crop stages, farm  
39 types, and years, this study reveals that generalist predators have potential to produce a stable,

40 predictable top-down effect on pests under various environmental conditions. As sustainable  
41 agriculture has become increasingly important, incorporating the ubiquitous generalist predators  
42 into pest management will likely open a promising avenue towards this goal.

43

44 *Keywords: biocontrol, trophic interactions, generalist predators, rice paddy, organic and*  
45 *conventional farms, stable isotope analysis*

46    1. Introduction

47              Using natural arthropod enemies for pest control has a long history in agriculture. The  
48       earliest record of biocontrol was documented in the book *Plants of the Southern Regions* (ca. 304  
49       A.D.): ~~It described people in Southern China selling sold~~ ants and their nests (~~attached to~~  
50       ~~branches~~) in the markets to control citrus insect pests (Huang and Yang, 1987). While  
51       ~~Nevertheless, with the advent of modern technologies in the past century,~~ synthetic pesticides  
52       have become the main method for controlling pests in ~~the past century~~ agriculture. ~~However,~~ this  
53       comes at a cost, such as posing risks to people, reducing biodiversity ~~(e.g., a decline in top~~  
54       ~~predators)~~ and hampering ecosystem functions ~~(e.g., a decline in pollinator service)~~ (Geiger *et al.*,  
55       2010; Kehoe *et al.*, 2017). As agriculture has become the largest land use type worldwide and a  
56       major driver for the global biodiversity crisis ~~and environmental degradation~~ in Anthropocene  
57       (Campbell *et al.*, 2017), a shift from synthetic pesticides to environmentally friendly practices  
58       (e.g., biocontrol) is urgently needed to make agriculture more sustainable (Gomiero *et al.*, 2011).  
59       For example, the European Commission has announced its plan to reduce the use of chemical  
60       pesticides in European Union agricultural systems by 50% by 2030 (European Commission,  
61       2020). To achieve this ambitious sustainability goal, biocontrol by natural enemies has been  
62       considered a key approach and has regained importance in modern agriculture.

63              Natural enemies used for pest control can be classified into two major groups based on  
64       their prey range: specialist and generalist predators. While specialist predators (e.g., parasitoid  
65       wasps) have been widely advocated in agriculture because they target specific pest species and  
66       produce less undesirable non-target effects (Stiling and Cornelissen, 2005), generalist predators  
67       (e.g., spiders) have been increasingly appreciated for their conspicuous existence and consistent  
68       biocontrol effect on pests (Symondson *et al.*, 2002; Stiling and Cornelissen, 2005; Michalko *et*

69 *al.*, 2019; Hsu *et al.*, 2021; Gajski *et al.*, 2023). For example, generalist predators were  
70 commonly reported in various agro-ecosystems and significantly reduced pest abundance in  
71 approximately 75% of cases in 181 field manipulative studies (Symondson *et al.*, 2002).  
72 Moreover, a meta-analysis suggests that generalist predators may exert stronger biocontrol  
73 effects on pest populations over time compared to specialists (Stiling and Cornelissen, 2005).

74 While the value of generalist predators has been increasingly appreciated, a few  
75 fundamental knowledge gaps need to be filled to validate their biocontrol potential and the  
76 underlying mechanisms in agro-ecosystems. For example, while studies have qualitatively  
77 analyzed the diets of generalist predators (e.g., using molecular gut content analysis to identify  
78 prey species) (Eitzinger and Traugott, 2011; Ingrao *et al.*, 2017; Albertini *et al.*, 2018), very few  
79 have quantified their diet composition over a growth season in the field (knowledge gap 1) (Hsu  
80 *et al.*, 2021; Otieno *et al.*, 2023). Quantifying their diet composition will provide critical  
81 information to help address the concern that generalist predators may switch their diet from pests  
82 to alternative prey and thus reduce their pest control effectiveness (Michalko *et al.*, 2019). For  
83 instance, if generalist predators still consume a high proportion of pests in their diet with the  
84 presence of alternative prey in the field, this result would help end a long debate on whether  
85 generalist predators serve well as biocontrol agents (Symondson *et al.*, 2002; Krey *et al.*, 2017;  
86 Michalko *et al.*, 2019). Moreover, examining the consistency of generalist predators in pest  
87 consumption in the field over years is important to assess the reliability of these predators as  
88 biocontrol agents in agriculture, although this information is lacking (knowledge gap 2). Given  
89 that temporal dynamics in population density or species composition commonly occur in agro-  
90 ecosystems (Settle *et al.*, 1996; Dominik *et al.*, 2018), a consistently high pest consumption by

91 generalist predators over years, if it occurs, will provide strong support for applying these  
92 predators in pest management programs.

93 To ~~better~~ understand the underlying mechanisms for the biocontrol effect of generalist  
94 predators, we also need to examine how various abiotic and biotic factors affect the diet  
95 composition of generalist predators in agro-ecosystems (knowledge gap 3). First, arthropod  
96 community composition (e.g., pest vs. alternative prey density) may vary with crop stages ~~ever~~  
97 ~~the growth season~~ and affect predator-prey trophic interactions (Roubinet *et al.*, 2017).

98 Therefore, we should examine how crop stage affects the pest consumption by generalist  
99 predators ~~to understand whether the role of these predators as biocontrol agents varies~~ within a  
100 growth season. Second, we should examine whether farming practices (e.g., organic and  
101 conventional) influence the diet composition of predators (e.g., pest consumption) (Birkhofer *et*  
102 *al.*, 2011). This will demonstrate whether generalist predators provide varying biocontrol values  
103 in specific farm types. ~~For examples, compared to conventional farming, organic farming may~~  
104 ~~promote arthropod diversity (Bengtsson *et al.*, 2005), potentially lowering the pest consumption~~  
105 ~~by generalist predators if predators shift their diet towards alternative prey. In contrast, the~~  
106 ~~application of synthetic chemicals in conventional farms may promote pest abundance (Hardin *et*~~  
107 ~~al., 1995; Settle *et al.*, 1996; Birkhofer *et al.*, 2008a; Guedes *et al.*, 2016), potentially leading to~~  
108 ~~higher pest consumption by predators.~~ Third, we should investigate the relationship between the  
109 relative prey abundance and the diet composition of their predators. This will clarify whether  
110 pest abundance or predator preference mainly explains the pest consumption by predators (Wise  
111 *et al.*, 2006; Kuusk and Ekbom, 2012; Roubinet *et al.*, 2017; Eitzinger *et al.*, 2019). Lastly, we  
112 should examine how surrounding vegetation (e.g., forest cover) affects the diet composition of  
113 generalist predators. While surrounding vegetation reportedly affected arthropod diversity and

114 predator-prey interactions in agro-ecosystems (Altieri and Letourneau, 1982; Altieri, 1999;  
115 Barbosa and Castellanos, 2005; Diehl *et al.*, 2013; Lichtenberg *et al.*, 2017), its effect on  
116 predators' diet composition is unclear. Understanding this will provide insights for managing the  
117 agricultural landscape and promoting biocontrol services by generalist predators.

118 To address these three knowledge gaps, this study aimed to 1) quantify the diet  
119 composition of generalist predators, 2) examine the consistency of predators in pest consumption  
120 over years, and 3) investigate how abiotic and biotic factors may affect the diet composition of  
121 these predators. Filling these gaps will provide insights for applying generalist predators in  
122 biocontrol programs. Specifically, this study sampled arthropod prey and generalist arthropod  
123 predators (GAPs) in sub-tropical organic and conventional rice farms over the rice growth season  
124 (seedling, tillering, flowering, and ripening stages) in central Miaoli County, Taiwan from 2017  
125 to 2019. The objectives of this study were to 1) quantify the diet composition of GAPs  
126 (ladybeetles and spiders) at each rice stage using stable isotope analysis ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ).  
127 Although GAPs may consume various prey items, we expected that GAPs would consistently  
128 consume a high proportion of pests in their diet at late crop stages (with high pest densities)  
129 regardless of years. We also expected that the diet composition of GAPs would be affected by,  
130 2) examine GAPs' consistency in pest consumption over years (i.e., the proportion of rice pests  
131 in GAPs' diets in 2017–2019), and 3) investigate how local abiotic and biotic factors (e.g., farm  
132 type, crop stage, percent forest cover, and the relative abundance of pests in the field) may affect  
133 pest consumption by GAPs. Stable isotope analysis has been widely applied in ecology to infer  
134 predator-prey trophic interactions and estimate the proportional contribution of different prey  
135 sources to predators' diets (Post, 2002; Boecklen *et al.*, 2011; Layman *et al.*, 2012). This  
136 quantification method reflects accumulated prey consumption in predators' diets, which may not

137 be achieved by some “snap-shot” techniques (e.g., field observations and molecular gut content  
138 analysis) (Newton, 2016).

139

140 **2. Materials and Methods**

141 *2.1. Study system and sample collection*

142 We collected terrestrial arthropods in paired organic and conventional rice farms in  
143 subtropical Taiwan (120.656-120.721 °E; 24.364-24.489 °N) from 2017 to 2019 (three farms  
144 pairseach in 2017 and seven farms pairs each in 2018 and 2019). While farms in the same pair  
145 were relatively close to each other (e.g., within a few hundred meters in distance), different farm  
146 pairs were at least 1 km apart from each other to reduce confounding effects. The sstudy farms  
147 (120.656-120.721 °E; 24.364-24.489 °N) were, averaged at 0.2 hectares on average and, were  
148 irrigated with surface water. The organic farms were managed with organic fertilizers (manure;  
149 2-3 applications/crop season) and natural pesticides (tea saponins; 1 application/crop season  
150 during the seedling or tillering stage). The conventional farms were managed with synthetic  
151 nitrogen fertilizers (2-3 applications/crop season) and organophosphate pesticides (1 application  
152 /crop season during the tillering or flowering stage). At each major rice crop stages (seedling,  
153 tillering, flowering, and ripening stages) during the growing season (April - July) in each study  
154 year, we collected arthropod samples by sweep-netting (36 cm in diameter with a mesh size of  
155 0.2 × 0.2 mm) the crop canopy 630 times in each of two transects inside a rice field. Each  
156 transect (ca 30 m long) was parallel to but 1.5m away from a randomly selected along the farm  
157 ridges. Samples were sealed in bags without chemical preservatives, iced, and transferred to  
158 refrigerator (-20°C) in the laboratory. We identified and counted arthropods under a dissecting

159 scope to the lowest possible taxonomic level (usually species, genus, or family). Main orders,  
160 families, and genera have been documented in Hsu et al. (Hsu *et al.*, 2021).

161

162 *2.2. Stable isotope analysis of arthropod samples*

163 After identification, arthropod samples were prepared for stable isotope analysis. First,  
164 samples were oven dried (50°C) for one week, ground, and weighed into individual tin capsules  
165 (5 × 9 mm). If necessary, several conspecifics would be pooled into a capsule to meet the  
166 minimum weight required for stable isotope analysis (i.e., 2 mg in this study). Stable isotope  
167 analysis (352 arthropod predator and 828 prey isotope samples) was conducted at the UC Davis  
168 Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ  
169 Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The standards for  
170 carbon and nitrogen stable isotope ratios were Vienna PeeDee Belemnite and atmospheric N<sub>2</sub>,  
171 respectively. The results of our samples were expressed in per mil (‰) relative to the  
172 international standards ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ).

173

174 *2.3. Arthropod trophic guild assignment*

175 A trophic guild represents a group of species using similar resources and forms a basic  
176 component of food webs. The concept has been proved to be practical in current ecology  
177 because it condenses broad taxonomic information into distinct functional groups in  
178 communities (Blondel, 2003). In this study, we classified arthropod samples into four trophic  
179 guilds (one predator and three prey guilds)based on their dietary information and isotope  
180 signatures: 1) “Predators” consisted of spiders and ladybeetles, which are the primary GAPs in  
181 rice farms. 2) “Rice herbivores” consisted of major rice pests, including planthoppers,

182 leafhoppers, and stink bugs. 3) “Tourist herbivores” consisted of herbivorous species without  
183 direct trophic association with rice plants, including some grasshoppers and leaf beetles. 4)  
184 “Detritivores” consisted of arthropods that feed on decaying organic material or plankton,  
185 including various midge and fly species. The classification of prey guilds was based on a  
186 combination of literature surveys and k-means clustering of stable isotope signatures of  
187 arthropod samples (see Appendix A: Fig. S1 for a stable isotope biplot for the three prey sources).  
188 The arthropod families/genera in each trophic guild are detailed in Appendix A: Table S1. This  
189 study focused on the trophic interactions between generalist predators and their prey sources and  
190 therefore did not consider less abundant trophic guilds (e.g., parasitoids) in subsequent analyses.  
191

#### 192 2.4. Data analyses

193 To quantify the diet composition of predators, we constructed a-Bayesian stable isotope  
194 mixing models using the R MixSIAR package (Stock and Semmens, 2016) to estimate the  
195 proportions of different prey sources (i.e., the three prey guilds including rice herbivores, tourist  
196 herbivores, and detritivores) in predators’ diet. In the mixing models, individual farm-year  
197 combination and crop stage were included as fixed effects for predator isotope data ~~to examine~~  
198 ~~their effects on predators’ diet composition~~; isotope data for the three prey guilds were pooled  
199 respectively to generate fixed source values ~~due to because of~~ their high mobility across farms  
200 (Mazzi and Dorn, 2012; Sun *et al.*, 2015). Isotope data at the seedling stage for the three study  
201 years were omitted from the analysis due to insufficient sample sizes for model estimation. To  
202 improve our model estimates, carbon and nitrogen concentration dependencies as well as the  
203 residual/process errors were incorporated (Phillips and Koch, 2002; Stock and Semmens, 2016).  
204 Trophic discrimination factors (TDFs) were estimated from the diet-dependent discrimination

205 equation proposed by Caut *et al.* (2009). We ran three Markov Chain Monte Carlo (MCMC)  
206 chains, each with 50,000 iterations and a burn-in number of 25,000, along with a non-  
207 informative Dirichlet prior. Chain convergence was assessed via Gelman-Rubin and Geweke  
208 diagnostics. Bayesian posterior median estimates of diet composition (for each farm-year-stage  
209 combination) were extracted for further analyses.

210 To examine how local abiotic and biotic factors (e.g., farm type, crop stage, percent  
211 forest cover, and the relative abundance of pests in the field) may affect the pest consumption by  
212 GAPs, we first fit generalized linear beta regression models (GLMs) with a beta distribution and  
213 a logit link function with year, farm type, crop stage, percent forest cover, and the relative  
214 abundance of rice herbivores as fixed effects without interactions and the proportion of rice  
215 herbivores consumed in predators' diet as the response variable using the R betareg package  
216 (Zeileis *et al.*, 2016),—with year, farm type, crop stage, percent forest cover, and the relative  
217 abundance of rice herbivores as fixed effects and the proportion of rice herbivores consumed in  
218 predators' diet as the response variable (i.e., posterior medians from the Bayesian stable isotope  
219 mixing models). We then refit the first model by adding the interaction terms among all the  
220 significant factors to create the final model. Model parameters were estimated using maximum  
221 likelihood, and their significance was analyzed via likelihood ratio test using the “Anova”  
222 function in the R car package (Fox and Weisberg, 2018). Tukey's post-hoc tests were performed  
223 for the significant factors using the “cld” function in the R emmeans package (Lenth and Lenth,  
224 2018). Note that †The percent forest cover around each study farm was estimated from Google  
225 Earth images by manually delimiting the forested areas within a 1-km radius circular buffer  
226 surrounding the farm and computing the fraction of these areas in the buffer zone. The 1-km  
227 radius was based on previous studies (Rusch *et al.*, 2016). Because spiders and ladybeetles were

228 the most abundant generalist predator groups in our study system and exhibited distinct foraging  
229 behavior (e.g., sit-and-wait vs. active hunting), we also performed all the aforementioned  
230 analyses separately for each of the two predator groups. All analyses were conducted in R  
231 version 4.0.3 (R Core Team, 2021).

232

### 233 3. Results

#### 234 3.1. Diet composition of predators in rice farms

235 Across organic and conventional farms during 2017-2019, the proportion of rice  
236 herbivores in all predators' diet increased over the course of the crop season from 231-47% at the  
237 tillering stage to 8079-975% at the ripening stage; the proportion of detritivores in predators' diet  
238 decreased from 358-6159% at the tillering stage to 1-2% at the ripening stage; the proportion of  
239 tourist herbivores in predators' diet also decreased from 135-202% at the tillering stage to 34-  
240 189% at the ripening stage (Fig. 1a; Appendix A: Table S2, Fig. S2).

241 Regarding individual predator groups, spiders and ladybeetles showed a marked  
242 difference in their diet composition over crop stages during 2017-2019. Across organic and  
243 conventional farms, spiders consumed a higher proportion of detritivores (313-55%) in their diet  
244 in the beginning of crop season (tillering stage) and substantially increased the consumption on  
245 rice herbivores to 78-954% in late crop season (ripening stage) (Fig. 1b; Appendix A: Table S2,  
246 Fig. S2). In contrast, ladybeetles in both organic and conventional farms consumed a low  
247 proportion of detritivores ( $\leq 817\%$ ) and a steadily high proportion of rice herbivores ( $\geq 8074\%$ )  
248 in their diet throughout the crop season (Fig. 1c; Appendix A: Table S2, Fig. S2). For both  
249 predator groups, tourist herbivores generally did not constitute an important prey source and

250 contributed less than 33% to the predators' diet of spiders and ladybeetles (Fig. 1b, 1c; Appendix  
251 A: Table S2, Fig. S2).  
252

253 *3.2. Patterns of rice herbivore consumption by predators*

254 We further analyzed rice herbivore consumption by GAPs since these herbivores are the  
255 main pests of concern. The patterns of rice herbivore consumption by both~~all~~ predators in  
256 organic and conventional rice farms were generally similar across the three study years,  
257 suggesting consistency in GAPs' feeding habits (Fig. 2). The consistency in herbivore  
258 consumption over years was also revealed by our beta regression model, which indicated that the  
259 proportion of rice herbivores consumed in all predators' diet did not vary across years ( $\chi^2 =$   
260 2.021.99,  $P = 0.367$ ; Table 1).

261 Interestingly, spiders and ladybeetles exhibited distinct within-season patterns of rice  
262 herbivore consumption. For spiders in organic and conventional farms, the proportion of rice  
263 herbivores in their diet increased toward later crop season, ranging from 1720–48% (tillering) to  
264 78–954% (ripening) (Fig. 2b; Appendix A: Table S2, Fig. S2), whereas for ladybeetles in organic  
265 and conventional farms, the proportion of rice herbivores in their diet remained relatively stable  
266 throughout the season, ranging from 8074–8593% (tilling) to 973–985% (ripening) (Fig. 2c;  
267 Appendix A: Table S2, Fig. S2).  
268

269 *3.3. Factors associated with rice herbivore consumption by predators*

270 The proportion of rice herbivores in GAPs' diet differed between organic and  
271 conventional farms for both(All predators:  $\chi^2 = 2045.198$ ,  $P < 0.001$ ) and Spiders:  $\chi^2 =$   
272 113.538,  $P < 0.001$ ) but not Ladybeetles:  $\chi^2 = 16.3570$ ,  $P = 0.25001$ ; Table 1). Specifically,

273 ~~both~~All predators consumed a higher proportion of rice herbivores in their diet in conventional vs.  
274 organic farms (Tukey's post-hoc test,  $P < 0.05$ ; Table 2), although spiders' diet was affected by  
275 a farm type-year interaction ( $\chi^2 = 7.64$ ,  $P = 0.02$ ; Table 2).

276 ———The proportion of rice herbivores in GAPs' diet also differed among crop stages (bothAll predators:  $\chi^2 = 22.57.4893$ ,  $P < 0.001$ ; spiders:  $\chi^2 = 95.93+15.43$ ,  $P < 0.001$ ;  
277 ladybeetles:  $\chi^2 = 15290.6094$ ,  $P < 0.001$ ; Table 1). Specifically, GAPs consumed higher  
278 proportions of rice herbivores in their diet at the flowering and/or ripening stage vs. the tillering  
279 stage (Tukey's post-hoc test,  $P < 0.05$ ; Table 3).

281 Different from previous studies showing the importance of surrounding landscape in  
282 determining arthropod community structure and pest control by predators (Rusch *et al.*, 2016),  
283 but see (Karp *et al.*, 2018), this study found no correlation between the proportion of rice  
284 herbivores consumed in GAPs' diet and the percent forest cover within a  
285 1-km radius buffer surrounding the study farms (bothAll predators:  $\chi^2 = 0.3061$ ,  $P = 0.4358$ ;  
286 spiders:  $\chi^2 = 0.954.28$ ,  $P = 0.3326$ ; ladybeetles:  $\chi^2 = 0.767$ ,  $P = 0.38$ ; Table 1). Furthermore,  
287 the proportion of rice herbivores consumed was not associated with the relative abundance of  
288 rice herbivores in the field (bothAll predators:  $\chi^2 = 0.0836$ ,  $P = 0.7755$ ; spiders:  $\chi^2 = 0.921.38$ ,  
289  $P = 0.324$ ; ladybeetles:  $\chi^2 = 1.150.93$ ,  $P = 0.2833$ ; Table 1).

#### 290 291 4. Discussion

292 Because the worldwide demand for environmentally friendly practices in agriculture has  
293 increased, we investigated the potential of GAPs (ubiquitous in nature) as biocontrol agents in  
294 agro-ecosystems. Specifically, we used stable isotopes to quantify the diet composition of GAPs  
295 in organic and conventional rice farms during the crop season in three consecutive years. Our

296 main results include the following: 1) Across the three study years, the rice herbivore  
297 consumption by GAPs increased in both organic and conventional farms over the crop season,  
298 from 293–47% at the tillering stage to 8079–957% at the ripening stage (Fig. 1a). The high  
299 percentage at the ripening stage indicates that GAPs could function as specialists in pest  
300 management during critical growth (late crop) stages. Notably, rice herbivore consumption by  
301 spiders increased gradually toward the later crop season (Fig. 2b), whereas the consumption by  
302 ladybeetles remained stable throughout the season (Fig. 2c). 2) Our results revealed similar  
303 among-year patterns in rice herbivore consumption by GAPs in organic and conventional rice  
304 farms, suggesting a consistency in GAPs' feeding habits and biocontrol value (Fig. 2, Table 1).  
305 3) The proportion of rice herbivores in GAPs' diets varied with farm type and crop stage (e.g.,  
306 higher in conventional farms and during flowering/ripening stages). However, contrary to results  
307 from previous studies, pest consumption by GAPs was not associated with surrounding  
308 landscape (e.g., percent forest cover) or the relative abundance of rice herbivores in the field  
309 (Table 1). We discuss in the following: 1) GAPs function as pest specialists at late crop stages, 2)  
310 GAPs exhibit consistent pest consumption patterns over years, 3) factors associated with pest  
311 consumption by predatorsGAPs, and 4) the potential caveats of this study (e.g., pest suppression  
312 and intraguild predation). We finish by highlighting the implications of our results for  
313 agricultural management.

314

315 *4.1. Generalist predators function as pest specialists at late crop stages*

316 While biocontrol, a farming practice with a long history, offers a promising solution for  
317 sustainable agriculture, the use of GAPs as biocontrol agents remains a concern because GAPs  
318 may switch diets between pests and alternative prey (Albajes and Alomar, 1999; Prasad and

319 Snyder, 2006; Roubinet *et al.*, 2018). This study addressed this concern and revealed a  
320 consistency in high pest consumption by GAPs at late crop stages over years. The results  
321 provide not only strong support for using GAPs in sustainable pest management, but also a novel  
322 aspect in biocontrol—generalist predators may function as guild-level specialist predators of  
323 pests during the late crop season. Specifically, across the three study years, GAPs in both  
324 organic and conventional farms consumed an increasing proportion of rice herbivores over the  
325 crop season, reaching 79.80-95.7% in predators' diet at the ripening stage, whereas the  
326 proportions of alternative prey (detritivores and tourist herbivores) in their diet gradually  
327 decreased below 24.18% at the ripening stage (Fig. 1<sup>15</sup>; Appendix A: Table S2, Fig. S2). The  
328 increase in rice herbivore consumption over time suggests that the biocontrol potential of  
329 predators increases toward late crop stages and peaks at the critical stage of crop production.  
330 This could be because of a higher herbivore (pest) density at late crop stages, suggested by a  
331 correlation between rice herbivore consumption and crop stage (see *Factors associated with pest*  
332 *consumption by predators*).

333 While GAPs consumed a high proportion of pests at late crop stages, the two predator  
334 groups in our study system, spiders and ladybeetles (Table S1), exhibited distinct dietary patterns  
335 over the crop season (Fig. 1, Fig. 2). Specifically, pest consumption by spiders increased  
336 substantially, but pest consumption by ladybeetles remained stable over the season (Fig. 2b vs.  
337 2c). This may be because different foraging modes—sit-and-wait (spiders) or actively hunting  
338 (ladybeetles)—can lead to different prey capture and thus diet composition (Nyffeler, 1999;  
339 Klecka and Boukal, 2013). For example, long-jawed orb-weavers (*Tetragnatha*), the most  
340 abundant genus in our spider samples, are sit-and-wait predators. The diet composition of these  
341 predators generally reflects prey availability (Nyffeler, 1999). In fact, spiders' diet composition

342 appeared to correlate with prey abundance in this study (Fig. 1b, Fig. 3), although crop stage,  
343 rather than pest abundance, better predicted the pest consumption by predators (see *Factors*  
344 associated with pest consumption by predators). In contrast, ladybeetles are actively hunting  
345 predators and may preferentially feed on rice herbivores, resulting in stable pest consumption  
346 over time (Fig. 1c, Fig. 2c, Fig. 3). Because predator foraging modes shape predator-prey-plant  
347 interactions (Schmitz, 2008), we suggest encourage future studies to examine different  
348 assemblages of sit-and-wait vs. actively hunting predators in field conditions to reveal the most  
349 efficient biocontrol practice over the entire crop season.

350

351 4.2. Generalists exhibit consistent pest consumption patterns over years

352 Ideal biocontrol agents provide a consistent, predictable effect on pests under various  
353 environmental conditions. Accordingly, GAPs in this study showed consistent pest consumption  
354 across years (Fig. 2), despite various abiotic and biotic environmental conditions. Specifically,  
355 regarding the abiotic factors, the daily mean temperature, particularly from April to June, varied  
356 substantially among years (Appendix A: Fig. S32). The daily precipitation also fluctuated over  
357 the three study years, with multiple high precipitation events in 2017, overall low precipitation in  
358 2018, and relatively uniform precipitation in 2019 (Appendix A: Fig. S32). Regarding the biotic  
359 factors, the composition of rice herbivores at the flowering and ripening stages differed  
360 substantially among the three years, in particular the two most dominant groups: leafhoppers  
361 (Cicadellidae/*Nephrotettix*) and planthoppers (Delphacidae/*Nilaparvata*) (Appendix A: Table S3).  
362 Although both abiotic and biotic factors varied substantially over the years of our study, pest  
363 consumption by GAPs generally remained stable, suggesting that GAPs can be a predictable,  
364 valuable tool for pest control in sustainable agriculture (but see Eitzinger *et al.*, 2021).

365

366 *4.3. Factors associated with pest consumption by predators*

367       The proportion of rice pests in GAPs' diets differed between farm types and among crop  
368       stages but was not associated with the percent forest cover surrounding the farms or the relative  
369       abundance of rice herbivores in the field (Table 1). Overall, GAPs in conventional farms  
370       consumed a higher proportion of rice pests in their diet compared ~~to with~~ those in organic farms  
371       (Table 2). There ~~may bear~~ two explanations for this: 1) Organic farming may promote  
372       arthropod diversity and therefore distract predators from feeding on target pests (Bengtsson *et al.*,  
373       2005; Birkhofer *et al.*, 2008b; Lichtenberg *et al.*, 2017). 2) Pest densities may be higher in  
374       conventional farms (Porcel *et al.*, 2018), ~~thus~~ leading to higher predator-prey encounter rates and  
375       ~~thus~~ pest consumption by GAPs. Regardless of the potential mechanisms, our results highlight  
376       the important but overlooked biocontrol value of GAPs in conventional farming systems.

377       Besides farming practices, ~~the~~ crop stages also affected pest consumption. Overall, pest  
378       consumption by GAPs increased from early (tillering) to late (ripening) stages (Fig. 2, Table 3),  
379       consistent with previous studies where predators consumed more pests in the late crop season  
380       (Roubinet *et al.*, 2017; Hsu *et al.*, 2021). ~~The underlying mechanisms in our study may be~~  
381       ~~summarized as follows: low pest density at the early crop stage led to low pest consumption by~~  
382       ~~GAPs; however, This may be because~~ pest populations increased with rice development and  
383       eventually predominated, leading to high pest consumption by GAPs at the flowering and  
384       ripening stages (Fig. 2 and 3). These findings indicate a higher biocontrol value of predators  
385       ~~during the middle and late crop seasons,~~ when the crop production is most vulnerable to pest  
386       damage. Therefore, farming practitioners may want to avoid practices that harm predators (e.g.,

387 chemical applications) during this period to maintain healthy predator populations and associated  
388 ecosystem services.

389 While habitat structure (e.g., surrounding vegetation) critically affects predator  
390 abundance and diversity (Altieri and Letourneau, 1982; Altieri, 1999; Diehl *et al.*, 2013;  
391 Lichtenberg *et al.*, 2017), its effect on the diet composition of predators remains unclear.  
392 Complex habitat structure (e.g., surrounding vegetation) has been suggested to promote predator  
393 abundance and diversity (Langelotto and Denno, 2004; Diehl *et al.*, 2013), but such higher  
394 complexity did not affect predators' diet composition in our study (Table 1). This might be  
395 because the prey species in our study system were mostly associated with rice plants but not the  
396 surrounding vegetation, consistent with a meta-analysis where habitat complexity had no effect  
397 on crop herbivore densities (Langelotto and Denno, 2004). Nevertheless, increasing vegetation  
398 complexity remains an important topic because it could benefit pest control by enhancing  
399 predator density and diversity.  
400 ——FurthermoreNotably, although the diet composition of generalist predators may  
401 correlated with prey availability in the field (Wise *et al.*, 2006; Hsu *et al.*, 2021), our beta  
402 regression models suggests no such correlation between rice herbivores and GAPs (Table 1). An  
403 explanation is that the relative abundance of rice herbivores was highly correlated with crop  
404 stage, a significant factor likely associating with various covariates (e.g., rice plant height) and  
405 explaining most variations in pest consumption by GAPs (Fig. 3, Table 1). We encourage  
406 further experiments, both observational and manipulative, to clarify the link between prey  
407 availability and generalist predators' diet composition in the field.  
408

409 *4.4. Potential caveats of this study*

410 Our study demonstrates high pest consumption by GAPs in rice fields over three years  
411 and examines the factors influencing GAPs' diet composition. While our study provides  
412 evidence for GAPs' biocontrol potential, some caveats may exist. First, high pest consumption  
413 in GAPs' diets does not necessarily imply a strong suppression of pest populations in the field,  
414 since pest population dynamics depend not only on the per capita effect of predators but also  
415 predator density and diversity (Letourneau *et al.*, 2009; Rusch *et al.*, 2016). To unveil the  
416 connection between per capita pest consumption and overall pest dynamics, future work may  
417 require complementing stable isotope analysis with field observations of predator and pest  
418 populations. Furthermore, future work may examine crop damage and production to reveal the  
419 effect of GAPs on pest control and crop performance. Second, while intra-guild predation  
420 potentially influences the pest control by GAPs (Straub *et al.*, 2008; Michalko *et al.*, 2019), it  
421 was not accounted for quantified in our diet composition analysis due to the limitation of stable  
422 isotope mixing models (Hsu *et al.*, 2021). However, this may not be a major concern in our  
423 study because rice plants grow as in dense clumps and form a complex structure that could  
424 substantially relax intra-guild predation pressure (Finke and Denno, 2006; Janssen *et al.*, 2007).  
425 Regardless, we caution that our diet estimates of predators (without predator-predator  
426 interference) might not apply to systems where intra-guild predation prevails.  
427

## 428 **5. Conclusions**

429 While biocontrol has been recognized as a valuable tool for sustainable agriculture,  
430 whether generalist predators can serve as effective biocontrol agents in pest management remains  
431 unclear. Our study helps solve this long-standing puzzle by using stable isotope analysis to  
432 quantify the diet composition of GAPs and identifying the underlying mechanisms for enemy-

433 pest interactions in rice farms over three consecutive years. The results show a high proportion  
434 of rice pests in GAPs' diets in both organic and conventional farms (e.g., 7980-957% at the  
435 ripening stage), suggesting that these generalist predators function as "pest specialists-predators"  
436 at late crop stages (when rice plants are fruiting and pests are abundant). The high pest  
437 consumption remained consistent across years regardless of climatic conditions, demonstrating  
438 the potential that generalist predators may produce a stable, predictable top-down effect on pests.  
439 Overall, our study lends support to applying generalist predators as biocontrol agents in both  
440 organic and conventional farms. As sustainable agriculture has become more important than  
441 ever in human history, incorporating the ubiquitous generalist predators into pest management,  
442 such as maintaining healthy populations of these predators, will likely open a promising avenue  
443 towards this goal.

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449

450    **Declaration of competing interest**

451        The authors declare that they have no known competing financial interests or personal  
452        relationships that could have appeared to influence the work reported in this paper.

453

454    **Data availability**

455        Data will be made available on request.

456

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462

463    **Author contributions**

464        All authors conducted the experiments; G.-C. Hsu and C.-K. Ho designed and wrote the  
465        manuscript; G.-C. Hsu and J.-A. Ou performed the statistical analyses.

466

467 **Appendix A. Supporting information**

468       Supplementary information associated with this article can be found in the online version  
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470

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628 **Table 1.** Statistical results from GLM beta regression models for examining the effects of  
 629 abiotic and biotic factors on pest consumption by all predators, spiders, and ladybeetles, and both  
 630 predators. Interactions were tested only between significant factors within each model.

Model	Factor	d.f.	$\chi^2$	P
<u>Both predators</u>	<u>Year</u>	<u>2</u>	<u>2.02</u>	<u>0.36</u>
	<u>Farm type</u>	<u>1</u>	<u>20.18</u>	<u>&lt; 0.001</u>
	<u>Crop stage</u>	<u>2</u>	<u>225.48</u>	<u>&lt; 0.001</u>
	<u>Percent forest cover</u>	<u>1</u>	<u>0.61</u>	<u>0.43</u>
	<u>Relative abundance of rice herbivores</u>	<u>1</u>	<u>0.08</u>	<u>0.77</u>
	<u>Spiders</u>	<u>2</u>	<u>7.58</u>	<u>0.02</u>
<u>Spiders</u>	<u>Year</u>	<u>1</u>	<u>11.58</u>	<u>&lt; 0.001</u>
	<u>Farm type</u>	<u>2</u>	<u>95.93</u>	<u>&lt; 0.001</u>
	<u>Crop stage</u>	<u>1</u>	<u>0.95</u>	<u>0.33</u>
	<u>Percent forest cover</u>	<u>1</u>	<u>0.92</u>	<u>0.34</u>
	<u>Ladybeetles</u>	<u>2</u>	<u>15.00</u>	<u>&lt; 0.001</u>
	<u>Year</u>	<u>1</u>	<u>1.35</u>	<u>0.25</u>
<u>Ladybeetles</u>	<u>Farm type</u>	<u>2</u>	<u>90.94</u>	<u>&lt; 0.001</u>
	<u>Crop stage</u>	<u>1</u>	<u>0.76</u>	<u>0.38</u>
	<u>Percent forest cover</u>	<u>1</u>	<u>1.15</u>	<u>0.28</u>

Model	Factor	d.f.	$\chi^2$	P
<u>All predators</u>	<u>Year</u>	<u>2</u>	<u>-1.99</u>	<u>-0.37</u>
	<u>Farm type</u>	<u>1</u>	<u>-15.98</u>	<u>&lt; 0.001</u>
	<u>Crop stage</u>	<u>2</u>	<u>227.93</u>	<u>&lt; 0.001</u>
	<u>Percent forest cover</u>	<u>1</u>	<u>-0.30</u>	<u>-0.58</u>
	<u>Relative abundance of rice herbivores</u>	<u>1</u>	<u>-0.36</u>	<u>-0.55</u>
	<u>Farm type × Crop stage</u>	<u>2</u>	<u>-2.06</u>	<u>-0.36</u>

<b>Spiders</b>	<b>Year</b>	2	<b>-7.92</b>	<b>-0.02</b>
	<b>Farm type</b>	+	<b>-13.38</b>	<b>&lt;0.001</b>
	<b>Crop stage</b>	2	<b>115.43</b>	<b>&lt;0.001</b>
	<b>Percent forest cover</b>	+	<b>-1.28</b>	<b>-0.26</b>
	<b>Relative abundance of rice herbivores</b>	+	<b>-1.38</b>	<b>-0.24</b>
	<b>Year × Farm type</b>	2	<b>-7.64</b>	<b>-0.02</b>
	<b>Year × Crop stage</b>	4	<b>-0.99</b>	<b>-0.91</b>
	<b>Farm type × Crop stage</b>	2	<b>-1.12</b>	<b>-0.57</b>
	<b>Year × Farm type × Crop stage</b>	4	<b>-0.44</b>	<b>-0.98</b>
<b>Ladybeetles</b>	<b>Year</b>	2	<b>-13.20</b>	<b>-0.001</b>
	<b>Farm type</b>	+	<b>-6.70</b>	<b>-0.001</b>
	<b>Crop stage</b>	2	<b>152.60</b>	<b>&lt;0.001</b>
	<b>Percent forest cover</b>	+	<b>-0.77</b>	<b>-0.38</b>
	<b>Relative abundance of rice herbivores</b>	+	<b>-0.93</b>	<b>-0.33</b>
	<b>Year × Farm type</b>	2	<b>-5.78</b>	<b>-0.06</b>
	<b>Year × Crop stage</b>	4	<b>-6.80</b>	<b>-0.15</b>
	<b>Farm type × Crop stage</b>	2	<b>-1.95</b>	<b>-0.38</b>
	<b>Year × Farm type × Crop stage</b>	4	<b>-2.37</b>	<b>-0.67</b>

634   **Table 2.** Tukey's post-hoc tests comparing the proportion of rice herbivores consumed in the  
 635   diet of predators in organic and conventional rice farms. Different superscript letters indicate  
 636   significant differences in the means of the posterior medians from Bayesian stable isotope  
 637   mixing models ( $\alpha = 0.05$ ) within each model.

Model	Farm type	Mean ( $\pm$ SE)	Lower 2.5%	Upper 2.5%
<u>BothAll</u> predators	Organic	0.66 <sup>a</sup> ( $\pm$ 0.02)	0.6 <sup>23</sup>	0.69
	Conventional	0.7 <sup>43</sup> <sup>b</sup> ( $\pm$ 0.0 <sup>24</sup> )	0.70	0.7 <sup>76</sup>
Spiders	Organic	0.64 <sup>a</sup> ( $\pm$ 0.02)	0. <sup>5960</sup>	0.68
	Conventional	0.73 <sup>b</sup> ( $\pm$ 0.02)	0.69	0.77
Ladybeetles	Organic	0. <u>9386</u> <sup>a</sup> ( $\pm$ 0.01)	0. <u>9285</u>	0. <u>9487</u>
	Conventional	0. <u>9488</u> <sup>ba</sup> ( $\pm$ 0.01)	0. <u>9387</u>	0. <u>9589</u>

638

639

640 **Table 3.** Tukey's post-hoc tests comparing the proportion of rice herbivores consumed in the  
 641 diet of predators at three crop stages (tillering, flowering, and ripening stages). Different  
 642 superscript letters indicate significant differences in the means of the posterior medians from  
 643 Bayesian stable isotope mixing models ( $\alpha = 0.05$ ) within each model.

Model	Crop stage	Mean ( $\pm$ SE)	Lower 2.5%	Upper 2.5%
<u>BothAll</u> predators	Tillering	0.3 <u>02</u> <sup>a</sup> ( $\pm$ 0.03)	0.2 <u>47</u>	0.3 <u>68</u>
	Flowering	0.8 <u>64</u> <sup>b</sup> ( $\pm$ 0.02)	0.8 <u>24</u>	0.8 <u>97</u>
	Ripening	0.9 <u>32</u> <sup>c</sup> ( $\pm$ 0.01)	0.9 <u>10</u>	0.9 <u>65</u>
Spiders	Tillering	0.3 <u>45</u> <sup>a</sup> ( $\pm$ 0.04)	0.2 <u>68</u>	0.42
	Flowering	0.8 <u>32</u> <sup>b</sup> ( $\pm$ 0.02)	0.78	0.8 <u>76</u>
	Ripening	0.8 <u>89</u> <sup>b</sup> ( $\pm$ 0.02)	0.8 <u>34</u>	0.93
Ladybeetles	Tillering	0.9 <u>18</u> <sup>a</sup> ( $\pm$ 0.01)	0.8 <u>90</u>	0.9 <u>28</u> <sup>a</sup>
	Flowering	0.9 <u>28</u> <sup>a</sup> ( $\pm$ 0.01)	0.9 <u>08</u> <sup>a</sup>	0.9 <u>48</u> <sup>a</sup>
	Ripening	0.9 <u>84</u> <sup>b</sup> ( $\pm$ 0.004)	0.9 <u>73</u>	0.9 <u>85</u>

644

645 **Figures (color should be used for Figure 1, 2, and 3)**

646 **Figure 1.** The proportions (mean  $\pm$  SE) of prey sources (rice herbivores, tourist herbivores, and  
647 detritivores) consumed in the diet of (a) ~~both~~all predators, (b) spiders, and (c) ladybeetles in  
648 organic and conventional rice farms over crop stages. The proportions were computed from the  
649 Bayesian posterior medians of diet estimates in replicate farms over the three study years.

650

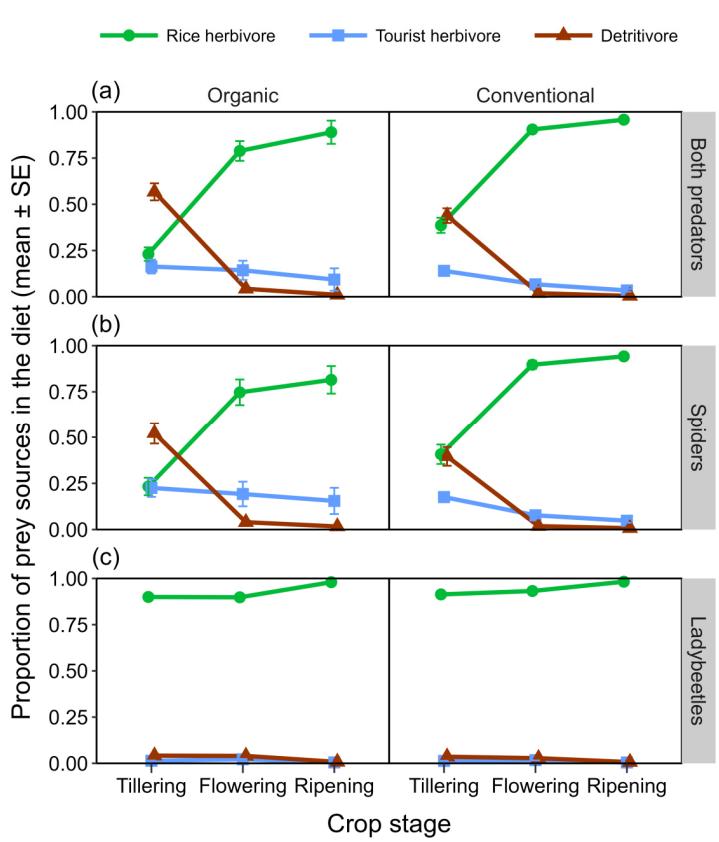
651 **Figure 2.** The proportion of rice herbivores consumed in the diet of (a) ~~all~~both predators, (b)  
652 spiders, and (c) ladybeetles in organic and conventional rice farms over crop stages in the three  
653 study years. The proportions were computed from the Bayesian posterior medians of diet  
654 estimates in replicate farms.

655

656 **Figure 3.** The relative abundance of prey sources in organic and conventional rice farms over  
657 crop stages during the three study years. The relative abundance was determined from the  
658 sweep-net samples pooled across replicate farms.

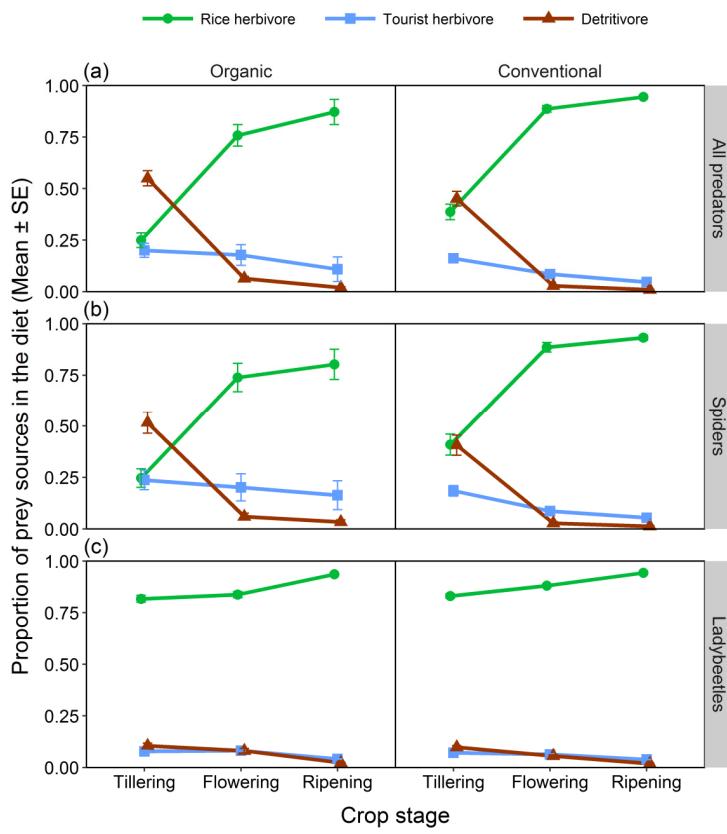
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660 **Figure 1.**



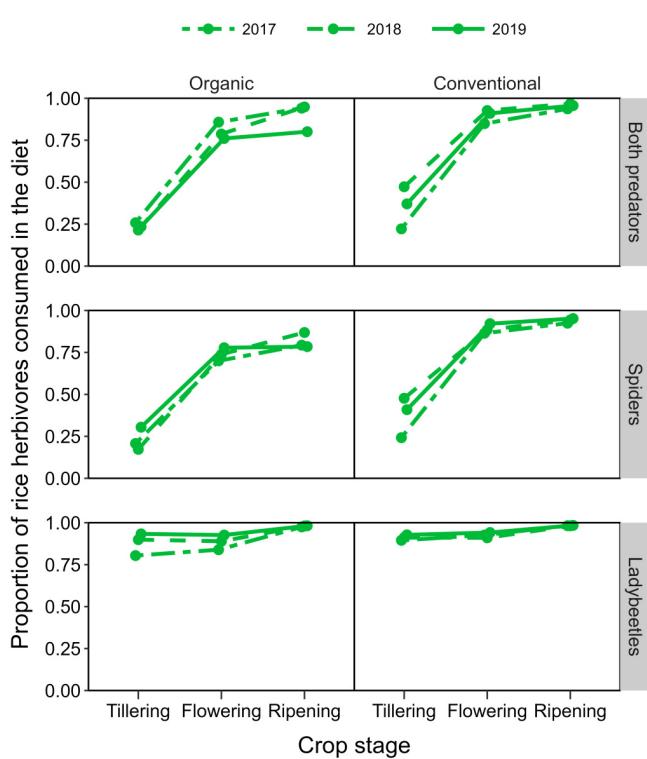
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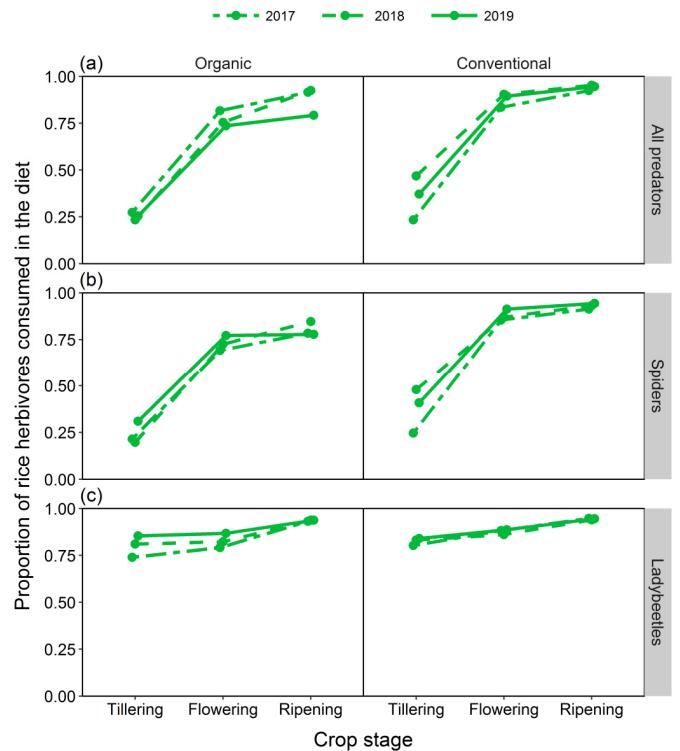


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664 **Figure 2.**



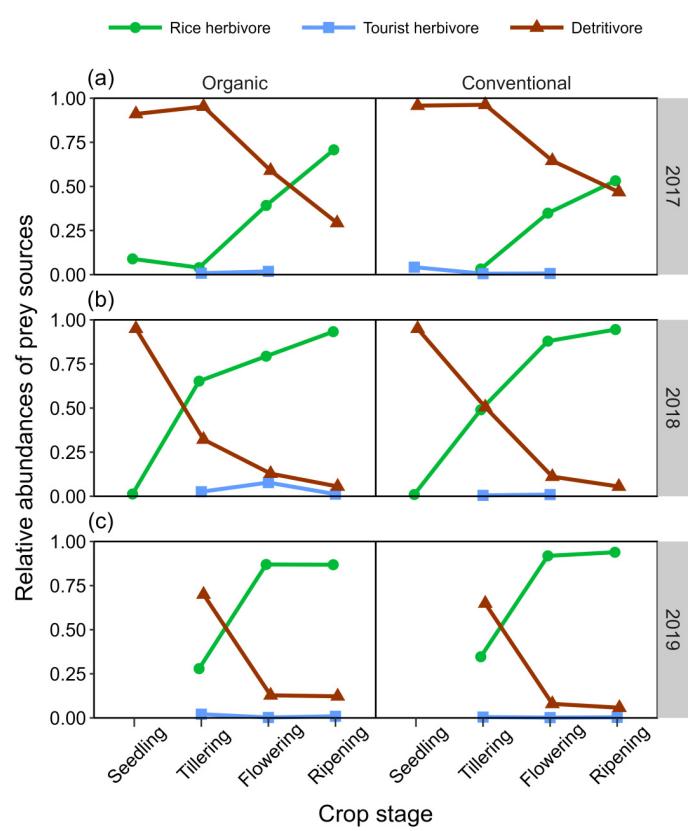
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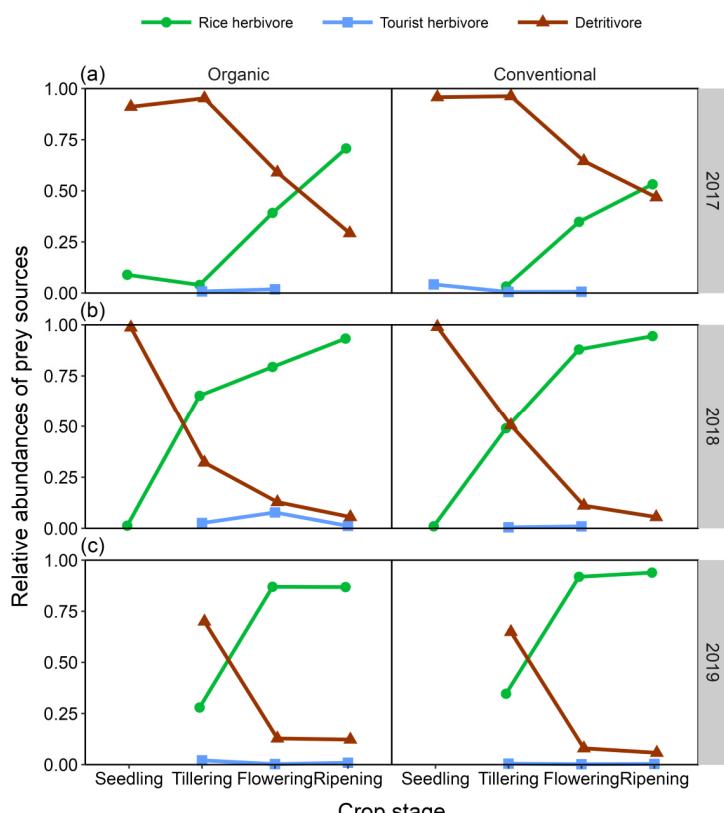
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668 **Figure 3.**



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1                    **Appendix A.**

2                    **A predator in need is a predator indeed: generalist arthropod predators**  
3                    **function as pest specialists at the late growth stage of rice**

4

5                    Gen-Chang Hsu<sup>1</sup>, Jia-Ang Ou<sup>2,3</sup>, Min-Hsuan Ni<sup>2</sup>, Zheng-Hong Lin<sup>2</sup> and Chuan-Kai Ho<sup>1,2\*</sup>

6

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10

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16 **Table S1.** The taxonomic information and trophic guilds of the arthropod samples in the three  
17 study years.

18 (a) Year 2017

Trophic guild	Order	Family/Genus
Predators	Araneae	Araneidae
	Araneae	Clubionidae
	Araneae	Oxyopidae
	Araneae	Tetragnathidae/ <i>Tetragnatha</i>
	Araneae	Thomisidae
	Coleoptera	Carabidae
	Coleoptera	Coccinellidae
Rice herbivores	Hemiptera	Cicadellidae/ <i>Nephrotettix</i>
	Hemiptera	Delphacidae/ <i>Nilaparvata</i>
	Hemiptera	Lygaeidae/ <i>Pachybrachius</i>
	Hemiptera	Pentatomidae/ <i>Scutinophara</i>
	Lepidoptera	Hesperiidae
	Lepidoptera	Pyralidae
	Lepidoptera	Nymphalidae
	Orthoptera	Pyrgomorphidae/ <i>Atractomorpha</i>
Tourist herbivores	Coleoptera	Chrysomelidae
	Orthoptera	Acrididae
Detritivores	Diptera	Chironomidae
	Diptera	Chloropidae
	Diptera	Ephydriidae
	Diptera	Muscidae
	Diptera	Sphaeroceridae
	Diptera	Stratiomyidae
	Diptera	Tephritidae

	Orthoptera	Tetrigidae
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19

20 (b) Year 2018

Trophic guild	Order	Family/Genus
Predators	Araneae	Araneidae
	Araneae	Clubionidae
	Araneae	Oxyopidae
	Araneae	Tetragnathidae/ <i>Tetragnatha</i>
	Araneae	Thomisidae
	Coleoptera	Coccinellidae
Rice herbivores	Hemiptera	Alydidae/ <i>Leptocorisa</i>
	Hemiptera	Cicadellidae/ <i>Nephrotettix</i>
	Hemiptera	Delphacidae/ <i>Nilaparvata</i>
	Hemiptera	Lygaeidae/ <i>Pachybrachius</i>
	Hemiptera	Pentatomidae/ <i>Scotinophara</i>
	Lepidoptera	Hesperiidae
	Lepidoptera	Pyralidae
Tourist herbivores	Orthoptera	Pyrgomorphidae/ <i>Atractomorpha</i>
	Coleoptera	Chrysomelidae
	Orthoptera	Acrididae
Detritivores	Diptera	Chironomidae
	Diptera	Chloropidae
	Diptera	Ephydriidae
	Diptera	Muscidae
	Diptera	Sciomyzidae
	Diptera	Stratiomyidae
	Orthoptera	Tetrigidae

21

22 (c) Year 2019

Trophic guild	Order	Family/Genus
Predators	Araneae	Araneidae
	Araneae	Clubionidae
	Araneae	Oxyopidae
	Araneae	Tetragnathidae/ <i>Tetragnatha</i>
	Araneae	Thomisidae
	Coleoptera	Coccinellidae
Rice herbivores	Diptera	Agromyzidae
	Hemiptera	Alydidae/ <i>Leptocoris</i>
	Hemiptera	Cicadellidae/ <i>Nephrotettix</i>
	Hemiptera	Coreidae
	Hemiptera	Delphacidae/ <i>Nilaparvata</i>
	Hemiptera	Lygaeidae/ <i>Pachybrachius</i>
	Hemiptera	Miridae
	Hemiptera	Pentatomidae/ <i>Scotinophara</i>
	Hemiptera	Ricaniidae
	Lepidoptera	Hesperiidae
	Lepidoptera	Nymphalidae
	Lepidoptera	Pyralidae
Tourist herbivores	Orthoptera	Pyrgomorphidae/ <i>Atractomorpha</i>
	Coleoptera	Chrysomelidae
Detritivores	Orthoptera	Acrididae
	Diptera	Calliphoridae
	Diptera	Chironomidae
	Diptera	Chloropidae
	Diptera	Ephydriidae
	Diptera	Lauxaniidae
	Diptera	Muscidae

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Diptera	Phoridae
Diptera	Platystomatidae
Diptera	Sarcophagidae
Diptera	Sciomyzidae
Diptera	Sphaeroceridae
Diptera	Stratiomyidae
Diptera	Tephritidae
Orthoptera	Tetrigidae
Orthoptera	Tridactylidae

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24 **Table S2.** The proportions (mean  $\pm$  SE) of prey sources (rice herbivores, tourist herbivores, and  
 25 detritivores) consumed in predators' diet in organic and conventional rice farms over crop stages  
 26 in each study year. The mean proportions were computed from the Bayesian posterior medians  
 27 of diet estimates in replicate farms;  $n$  represents the number of replicate farms for the diet  
 28 estimation. Note that the differences in  $n$  within the same study year were due to the absence of  
 29 predators in the sweep-net samples in some replicate farms).

Year	Farm type	Crop stage	Predator	Prey source			$n$
				Rice herbivore	Tourist herbivore	Detritivore	
2017	Organic	Tillering	Both	<u>0.26 ± 0.08</u>	<u>0.15 ± 0.05</u>	<u>0.54 ± 0.13</u>	<u>3</u>
			Spiders	<u>0.21 ± 0.13</u>	<u>0.33 ± 0.17</u>	<u>0.44 ± 0.19</u>	<u>3</u>
			Ladybeetles	<u>0.80</u>	<u>0.02</u>	<u>0.08</u>	<u>1</u>
		Flowering	Both	<u>0.86 ± 0.03</u>	<u>0.09 ± 0.02</u>	<u>0.04 ± 0.02</u>	<u>3</u>
			Spiders	<u>0.70 ± 0.15</u>	<u>0.24 ± 0.16</u>	<u>0.04 ± 0.03</u>	<u>3</u>
			Ladybeetles	<u>0.84</u>	<u>0.03</u>	<u>0.07</u>	<u>1</u>
		Ripening	Both	<u>0.94 ± 0.01</u>	<u>0.04 ± 0.01</u>	<u>0.01 ± 0.01</u>	<u>3</u>
			Spiders	<u>0.79 ± 0.12</u>	<u>0.18 ± 0.12</u>	<u>0.02 ± 0.01</u>	<u>3</u>
			Ladybeetles	<u>0.97 ± 0.01</u>	<u>0.01 ± 0.00</u>	<u>0.01 ± 0.00</u>	<u>3</u>
	Conventional	Tillering	Both	<u>0.22 ± 0.02</u>	<u>0.15 ± 0.05</u>	<u>0.60 ± 0.05</u>	<u>3</u>
			Spiders	<u>0.24 ± 0.01</u>	<u>0.20 ± 0.07</u>	<u>0.55 ± 0.08</u>	<u>3</u>
			Ladybeetles	<u>0.90</u>	<u>0.01</u>	<u>0.04</u>	<u>1</u>
		Flowering	Both	<u>0.85 ± 0.03</u>	<u>0.1 ± 0.03</u>	<u>0.03 ± 0.01</u>	<u>3</u>
			Spiders	<u>0.86 ± 0.02</u>	<u>0.1 ± 0.03</u>	<u>0.03 ± 0.01</u>	<u>3</u>
			Ladybeetles	<u>0.93 ± 0.01</u>	<u>0.02 ± 0.00</u>	<u>0.03 ± 0.00</u>	<u>2</u>
		Ripening	Both	<u>0.94 ± 0.02</u>	<u>0.05 ± 0.02</u>	<u>0.01 ± 0.00</u>	<u>3</u>
			Spiders	<u>0.92 ± 0.02</u>	<u>0.06 ± 0.02</u>	<u>0.01 ± 0.00</u>	<u>3</u>
			Ladybeetles	<u>0.98 ± 0.00</u>	<u>0.00 ± 0.00</u>	<u>0.01 ± 0.00</u>	<u>2</u>
2018	Organic	Tillering	Both	<u>0.21 ± 0.04</u>	<u>0.20 ± 0.07</u>	<u>0.54 ± 0.07</u>	<u>7</u>
			Spiders	<u>0.17 ± 0.03</u>	<u>0.26 ± 0.08</u>	<u>0.54 ± 0.08</u>	<u>7</u>
			Ladybeetles	<u>0.90 ± 0.02</u>	<u>0.01 ± 0.00</u>	<u>0.04 ± 0.01</u>	<u>6</u>
		Flowering	Both	<u>0.79 ± 0.04</u>	<u>0.14 ± 0.04</u>	<u>0.04 ± 0.01</u>	<u>6</u>
			Spiders	<u>0.74 ± 0.07</u>	<u>0.18 ± 0.07</u>	<u>0.04 ± 0.01</u>	<u>5</u>

2019	Conventional	<u>Ripening</u>	<u>Ladybeetles</u>	<u>0.89 ± 0.01</u>	<u>0.02 ± 0.00</u>	<u>0.04 ± 0.01</u>	<u>3</u>
			<u>Both</u>	<u>0.95 ± 0.01</u>	<u>0.03 ± 0.01</u>	<u>0.01 ± 0.00</u>	<u>5</u>
			<u>Spiders</u>	<u>0.87 ± 0.04</u>	<u>0.09 ± 0.02</u>	<u>0.02 ± 0.01</u>	<u>4</u>
		<u>Tillering</u>	<u>Ladybeetles</u>	<u>0.98 ± 0.00</u>	<u>0.00 ± 0.00</u>	<u>0.01 ± 0.00</u>	<u>5</u>
			<u>Both</u>	<u>0.47 ± 0.08</u>	<u>0.12 ± 0.02</u>	<u>0.35 ± 0.05</u>	<u>7</u>
			<u>Spiders</u>	<u>0.48 ± 0.11</u>	<u>0.18 ± 0.03</u>	<u>0.31 ± 0.08</u>	<u>7</u>
		<u>Flowering</u>	<u>Ladybeetles</u>	<u>0.91 ± 0.01</u>	<u>0.01 ± 0.00</u>	<u>0.04 ± 0.01</u>	<u>4</u>
			<u>Both</u>	<u>0.93 ± 0.03</u>	<u>0.05 ± 0.02</u>	<u>0.01 ± 0.00</u>	<u>6</u>
			<u>Spiders</u>	<u>0.88 ± 0.05</u>	<u>0.09 ± 0.04</u>	<u>0.01 ± 0.01</u>	<u>6</u>
	Organic	<u>Ripening</u>	<u>Ladybeetles</u>	<u>0.91 ± 0.03</u>	<u>0.02 ± 0.00</u>	<u>0.04 ± 0.01</u>	<u>2</u>
			<u>Both</u>	<u>0.97 ± 0.01</u>	<u>0.03 ± 0.01</u>	<u>0.00 ± 0.00</u>	<u>7</u>
			<u>Spiders</u>	<u>0.94 ± 0.04</u>	<u>0.05 ± 0.04</u>	<u>0.00 ± 0.00</u>	<u>2</u>
		<u>Tillering</u>	<u>Ladybeetles</u>	<u>0.98 ± 0.00</u>	<u>0.00 ± 0.00</u>	<u>0.01 ± 0.00</u>	<u>5</u>
			<u>Both</u>	<u>0.23 ± 0.08</u>	<u>0.13 ± 0.06</u>	<u>0.61 ± 0.08</u>	<u>7</u>
			<u>Spiders</u>	<u>0.30 ± 0.10</u>	<u>0.14 ± 0.05</u>	<u>0.54 ± 0.09</u>	<u>7</u>
		<u>Flowering</u>	<u>Ladybeetles</u>	<u>0.93 ± 0.03</u>	<u>0.01 ± 0.00</u>	<u>0.03 ± 0.01</u>	<u>3</u>
			<u>Both</u>	<u>0.76 ± 0.12</u>	<u>0.17 ± 0.12</u>	<u>0.05 ± 0.01</u>	<u>7</u>
			<u>Spiders</u>	<u>0.78 ± 0.15</u>	<u>0.18 ± 0.14</u>	<u>0.04 ± 0.01</u>	<u>6</u>
	Conventional	<u>Ripening</u>	<u>Ladybeetles</u>	<u>0.93 ± 0.02</u>	<u>0.02 ± 0.00</u>	<u>0.03 ± 0.01</u>	<u>3</u>
			<u>Both</u>	<u>0.80 ± 0.17</u>	<u>0.18 ± 0.16</u>	<u>0.01 ± 0.00</u>	<u>5</u>
			<u>Spiders</u>	<u>0.78 ± 0.17</u>	<u>0.19 ± 0.16</u>	<u>0.02 ± 0.01</u>	<u>5</u>
		<u>Tillering</u>	<u>Ladybeetles</u>	<u>0.98 ± 0.00</u>	<u>0.00 ± 0.00</u>	<u>0.01 ± 0.00</u>	<u>5</u>
			<u>Both</u>	<u>0.37 ± 0.04</u>	<u>0.15 ± 0.05</u>	<u>0.46 ± 0.06</u>	<u>7</u>
			<u>Spiders</u>	<u>0.41 ± 0.06</u>	<u>0.16 ± 0.05</u>	<u>0.42 ± 0.08</u>	<u>7</u>
		<u>Flowering</u>	<u>Ladybeetles</u>	<u>0.93 ± 0.00</u>	<u>0.01 ± 0.00</u>	<u>0.03 ± 0.00</u>	<u>2</u>
			<u>Both</u>	<u>0.91 ± 0.02</u>	<u>0.06 ± 0.02</u>	<u>0.02 ± 0.00</u>	<u>7</u>
			<u>Spiders</u>	<u>0.92 ± 0.02</u>	<u>0.06 ± 0.02</u>	<u>0.02 ± 0.01</u>	<u>7</u>
		<u>Ripening</u>	<u>Ladybeetles</u>	<u>0.94 ± 0.00</u>	<u>0.02 ± 0.00</u>	<u>0.02 ± 0.00</u>	<u>6</u>
			<u>Both</u>	<u>0.96 ± 0.01</u>	<u>0.04 ± 0.01</u>	<u>0.00 ± 0.00</u>	<u>5</u>
			<u>Spiders</u>	<u>0.95 ± 0.02</u>	<u>0.04 ± 0.02</u>	<u>0.01 ± 0.00</u>	<u>5</u>
			<u>Ladybeetles</u>	<u>0.98 ± 0.00</u>	<u>0.00 ± 0.00</u>	<u>0.01 ± 0.00</u>	<u>3</u>

Year	Farm type	Crop stage	Predator	Source			#
				Rice herbivore	Tourist herbivore	Detritivore	
2017	Organic	Tillering	All	0.27 ± 0.08	0.19 ± 0.05	0.54 ± 0.12	3
			Spider	0.21 ± 0.13	0.33 ± 0.16	0.46 ± 0.18	3
			Ladybeetle	0.74	0.09	0.17	4
		Flowering	All	0.82 ± 0.04	0.13 ± 0.04	0.05 ± 0.03	3
			Spider	0.69 ± 0.15	0.25 ± 0.15	0.06 ± 0.04	3
			Ladybeetle	0.79	0.09	0.12	4
		Ripening	All	0.92 ± 0.02	0.07 ± 0.02	0.02 ± 0.01	3
			Spider	0.78 ± 0.12	0.19 ± 0.12	0.03 ± 0.02	3
			Ladybeetle	0.93 ± 0.01	0.04 ± 0.01	0.03 ± 0.01	3
2018	Conventional	Tillering	All	0.23 ± 0.01	0.17 ± 0.05	0.59 ± 0.05	3
			Spider	0.25 ± 0.01	0.2 ± 0.06	0.55 ± 0.08	3
			Ladybeetle	0.80	0.08	0.12	4
		Flowering	All	0.83 ± 0.03	0.12 ± 0.03	0.05 ± 0.01	3
			Spider	0.85 ± 0.02	0.11 ± 0.03	0.04 ± 0.01	3
			Ladybeetle	0.88 ± 0.02	0.06 ± 0.01	0.06 ± 0.01	2
		Ripening	All	0.92 ± 0.02	0.06 ± 0.02	0.02 ± 0.01	3
			Spider	0.91 ± 0.01	0.07 ± 0.02	0.02 ± 0.01	3
			Ladybeetle	0.95 ± 0.01	0.04 ± 0.01	0.02 ± 0.01	2
	Organic	Tillering	All	0.23 ± 0.03	0.22 ± 0.05	0.55 ± 0.06	7
			Spider	0.20 ± 0.02	0.28 ± 0.07	0.52 ± 0.07	7
			Ladybeetle	0.81 ± 0.02	0.08 ± 0.01	0.11 ± 0.01	6
		Flowering	All	0.75 ± 0.04	0.17 ± 0.04	0.07 ± 0.02	6
			Spider	0.73 ± 0.07	0.20 ± 0.07	0.08 ± 0.04	5
			Ladybeetle	0.82 ± 0.01	0.09 ± 0.01	0.09 ± 0.01	3
		Ripening	All	0.92 ± 0.02	0.05 ± 0.01	0.02 ± 0.01	5
			Spider	0.85 ± 0.04	0.11 ± 0.03	0.05 ± 0.03	4
			Ladybeetle	0.94 ± 0.01	0.04 ± 0.01	0.02 ± 0.01	5
	Conventional	Tillering	All	0.47 ± 0.07	0.15 ± 0.02	0.38 ± 0.05	7

2019	Organic	Flowering	Spider	$0.48 \pm 0.10$	$0.19 \pm 0.03$
			Ladybeetle	$0.83 \pm 0.02$	$0.07 \pm 0.01$
			All	$0.90 \pm 0.03$	$0.07 \pm 0.02$
		Ripening	Spider	$0.87 \pm 0.06$	$0.10 \pm 0.04$
			Ladybeetle	$0.86 \pm 0.03$	$0.07 \pm 0.01$
		Tillering	All	$0.95 \pm 0.01$	$0.04 \pm 0.01$
			Spider	$0.93 \pm 0.05$	$0.06 \pm 0.04$
			Ladybeetle	$0.94 \pm 0.01$	$0.04 \pm 0.01$
	Conventional	Flowering	All	$0.25 \pm 0.08$	$0.19 \pm 0.06$
			Spider	$0.31 \pm 0.10$	$0.15 \pm 0.06$
			Ladybeetle	$0.85 \pm 0.04$	$0.08 \pm 0.01$
		Ripening	All	$0.74 \pm 0.12$	$0.20 \pm 0.11$
			Spider	$0.77 \pm 0.15$	$0.18 \pm 0.14$
			Ladybeetle	$0.87 \pm 0.02$	$0.07 \pm 0.01$
		Tillering	All	$0.79 \pm 0.16$	$0.19 \pm 0.16$
			Spider	$0.78 \pm 0.17$	$0.19 \pm 0.16$
			Ladybeetle	$0.94 \pm 0.01$	$0.04 \pm 0.01$

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34   **Table S3.** The relative abundance of the major families/genera in rice herbivore guild at the  
35   flowering and ripening stages in the three study years. Samples were pooled across ~~the~~-replicate  
36   farms.

37   (a) Flowering stage

Family/Genus	Year 2017	Year 2018	Year 2019
Cicadellidae/ <i>Nephrotettix</i>	7.6%	22.5%	69.7%
Delphacidae/ <i>Nilaparvata</i>	88.2%	71.9%	25.4%
Lygaeidae/ <i>Pachybrachius</i>	NA	0.8%	1.3%
Pentatomidae/ <i>Scotinophara</i>	0.8%	2.9%	0.8%
Others	3.4%	1.9%	2.8%
<i>Total</i>	100%	100%	100%

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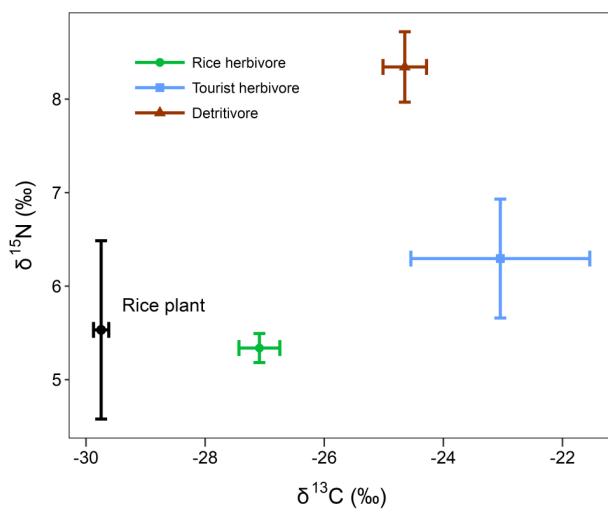
39   (b) Ripening stage

Family/Genus	Year 2017	Year 2018	Year 2019
Cicadellidae/ <i>Nephrotettix</i>	69.4%	74.9%	83.5%
Delphacidae/ <i>Nilaparvata</i>	28.9%	13.4%	6.2%
Lygaeidae/ <i>Pachybrachius</i>	NA	0.2%	4.1%
Pentatomidae/ <i>Scotinophara</i>	1.7%	10.4%	4.5%
Others	NA	1.1%	1.7%
<i>Total</i>	100%	100%	100%

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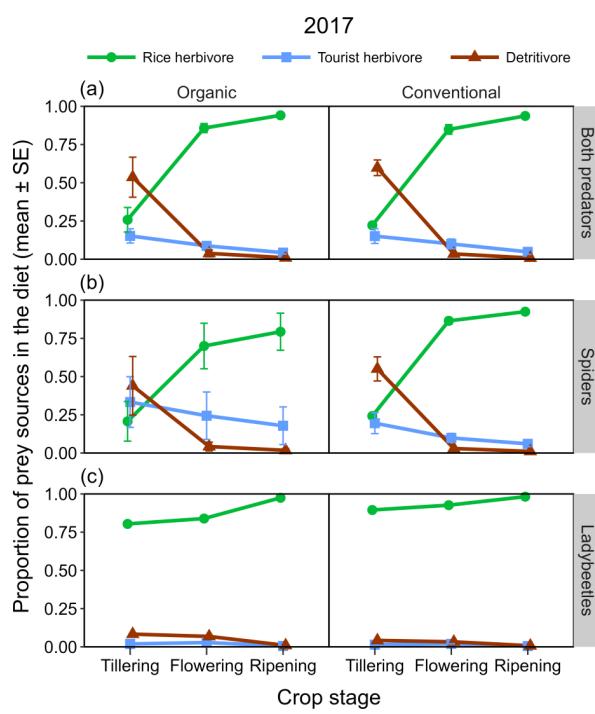
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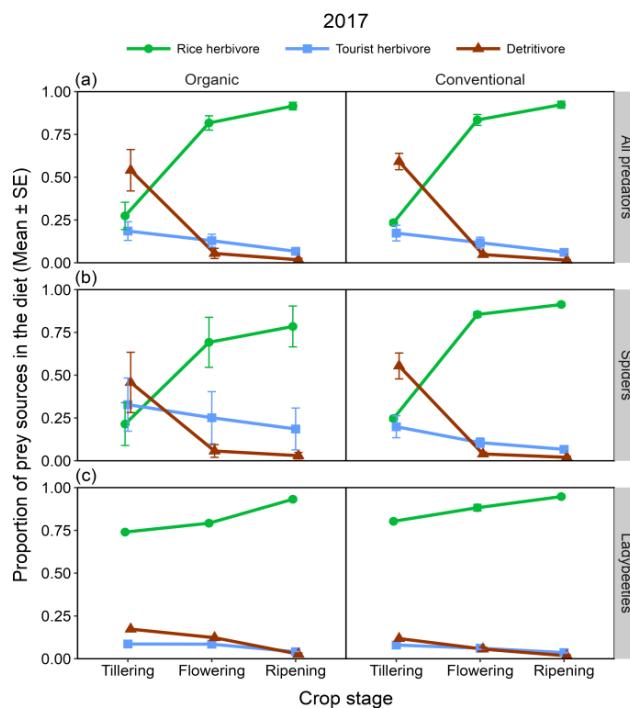
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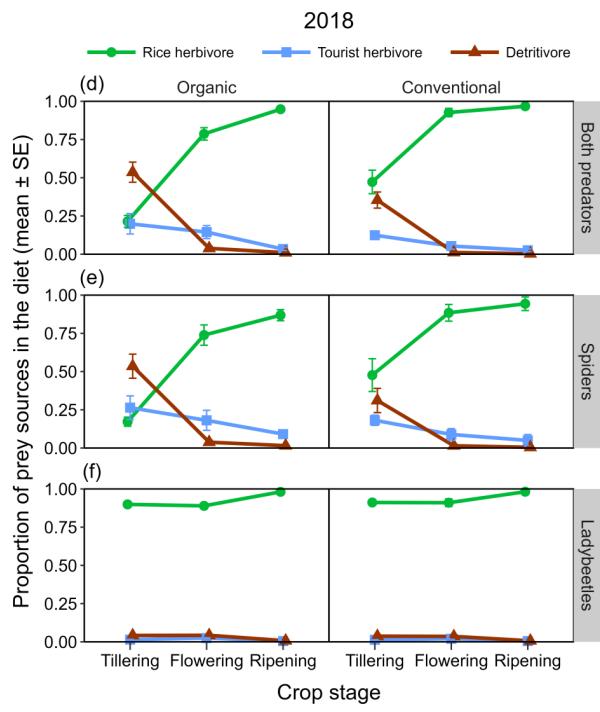
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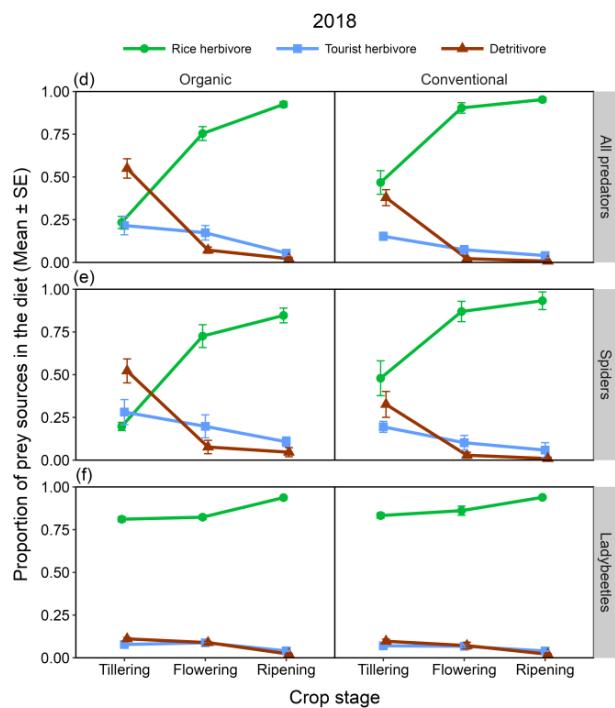




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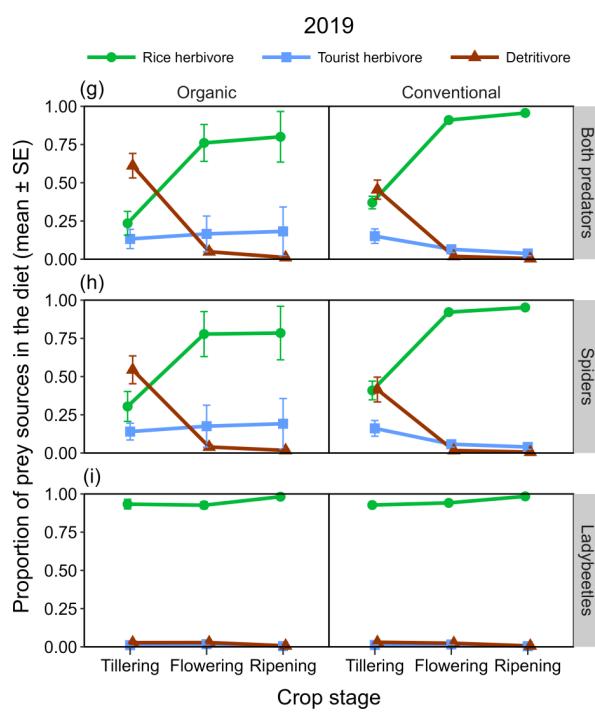


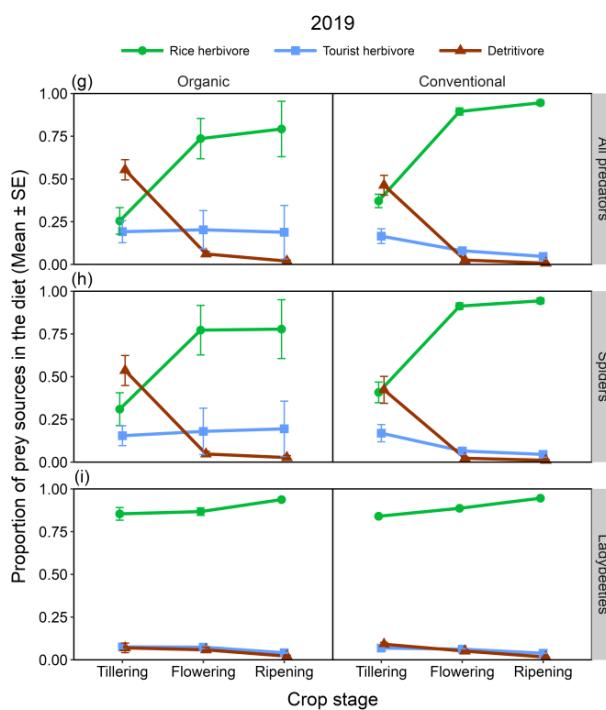


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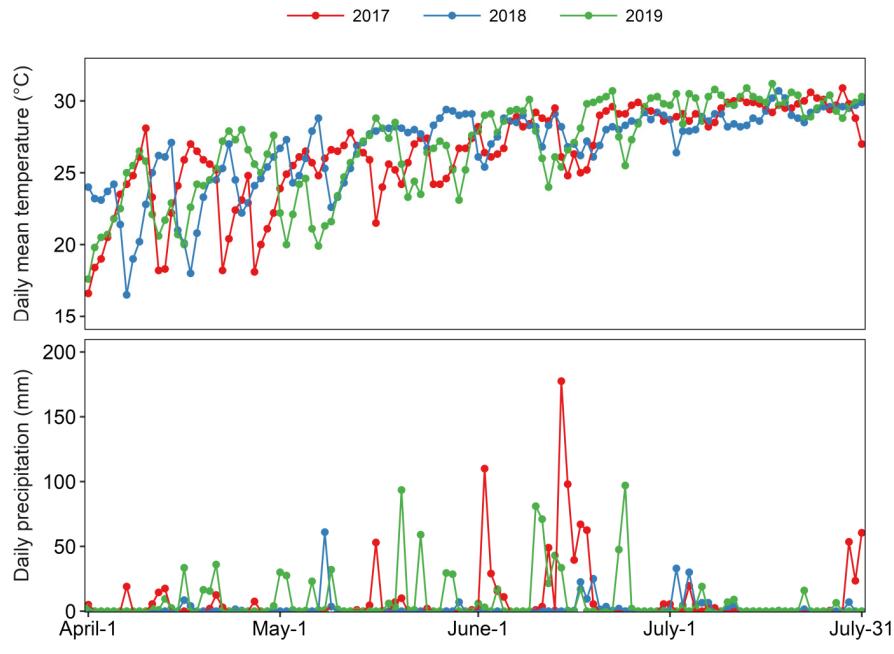




54

55 **Figure S24.** The proportions (mean  $\pm$  SE) of prey sources (rice herbivores, tourist herbivores,  
 56 detritivores) consumed in the diet of predators in organic and conventional rice farms over crop  
 57 stages in each study year: (a), (d), and (g) indicate both all predators ([spiders and ladybeetles](#)) as a  
 58 whole feeding guild; (b), (e), and (h) indicate spiders; (c), (f), and (i) indicate ladybeetles. The  
 59 proportions were computed from the Bayesian posterior [medians of diet estimates in means of](#)  
 60 replicate farms.

61



62

63 **Figure S32.** Daily mean temperature and precipitation of the study sites during the rice growth  
 64 season (April to July) of the three study years. Observation data from the closest local weather  
 65 station (Yuanli station) to the study farms were retrieved from the Central Weather Bureau  
 66 Observation Data Inquire System (<https://e-service.cwb.gov.tw/HistoryDataQuery/index.jsp>).

## Highlights

- We analyzed arthropod isotope samples in organic/conventional rice farms
- Generalist arthropod predators (GAPs) act as pest specialists at late crop stages
- The high pest consumption by GAPs is consistent across years (climates) and farms
- The results lend supports to applying GAPs as biocontrol agents in agroecosystems

## 1 *Submission type: Research article*

2

# 3 A predator in need is a predator indeed: generalist arthropod predators

## 4 function as pest specialists at the late growth stage of rice

5

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17

## Abstract

18 Biocontrol, using natural enemies for pest control, has a long history in agriculture. It has  
19 received a surge of interest in the recent Anthropocene because of its potential as a valuable tool  
20 for sustainable agriculture. To solve a long-standing puzzle in biocontrol—how well the  
21 ubiquitous generalist arthropod predators (GAPs) function as biocontrol agents—this study  
22 aimed to 1) quantify the diet composition of GAPs at each crop stage using stable isotope  
23 analysis, 2) examine the consistency of GAPs in pest consumption over years, and 3) investigate  
24 how abiotic and biotic factors affect pest consumption by GAPs. Specifically, we sampled  
25 arthropod prey and GAPs in sub-tropical organic and conventional rice farms over crop stages  
26 (seedling, tillering, flowering, and ripening) in three consecutive years. Among our field-  
27 collected samples, 352 arthropod predator and 828 prey isotope samples were analyzed to infer  
28 predator-prey interactions. Our results show the following: a) The proportion of rice pests in  
29 GAPs' diets in both organic and conventional farms increased over the crop season, from 21-  
30 47% at the tillering stage to 80-97% at the ripening stage, across the three study years. The high  
31 percentage in pest consumption at late crop stages (flowering and ripening) suggests that GAPs  
32 can function as specialists in pest management during the critical period of crop production.  
33 Regarding individual predator groups, spiders and ladybeetles exhibited distinct dietary patterns  
34 over crop stages. b) The high pest consumption by GAPs at late crop stages was similar across  
35 years (with different climatic conditions), suggesting a consistency in GAP feeding habits and  
36 biocontrol value. c) The proportion of rice pests in GAPs' diets varied with farm type and crop  
37 stage (e.g., higher in conventional farms and during flowering/ripening stages). By quantifying  
38 the diet composition of GAPs over crop stages, farm types, and years, this study reveals that  
39 generalist predators have potential to produce a stable, predictable top-down effect on pests

40 under various environmental conditions. As sustainable agriculture has become increasingly  
41 important, incorporating the ubiquitous generalist predators into pest management will likely  
42 open a promising avenue towards this goal.

43

44 *Keywords: biocontrol, trophic interactions, generalist predators, rice paddy, organic and*  
45 *conventional farms, stable isotope analysis*

46     **1. Introduction**

47         Using natural arthropod enemies for pest control has a long history in agriculture. The  
48         earliest record of biocontrol was documented in the book *Plants of the Southern Regions* (ca. 304  
49         A.D.): people sold ants and their nests in the markets to control citrus insect pests (Huang and  
50         Yang, 1987). While synthetic pesticides have become the main method for controlling pests in  
51         the past century, this comes at a cost, such as posing risks to people, reducing biodiversity and  
52         hampering ecosystem functions (Geiger *et al.*, 2010; Kehoe *et al.*, 2017). As agriculture has  
53         become the largest land use type worldwide and a major driver for the global biodiversity crisis  
54         in Anthropocene (Campbell *et al.*, 2017), a shift from synthetic pesticides to environmentally  
55         friendly practices (e.g., biocontrol) is urgently needed to make agriculture more sustainable  
56         (Gomiero *et al.*, 2011). For example, the European Commission has announced its plan to  
57         reduce the use of chemical pesticides in European Union agricultural systems by 50% by 2030  
58         (European Commission, 2020). To achieve this ambitious sustainability goal, biocontrol by  
59         natural enemies has been considered a key approach and has regained importance in modern  
60         agriculture.

61         Natural enemies used for pest control can be classified into two major groups based on  
62         their prey range: specialist and generalist predators. While specialist predators (e.g., parasitoid  
63         wasps) have been widely advocated in agriculture because they target specific pest species and  
64         produce less undesirable non-target effects (Stiling and Cornelissen, 2005), generalist predators  
65         (e.g., spiders) have been increasingly appreciated for their conspicuous existence and consistent  
66         biocontrol effect on pests (Symondson *et al.*, 2002; Stiling and Cornelissen, 2005; Michalko *et*  
67         *al.*, 2019; Hsu *et al.*, 2021; Gajski *et al.*, 2023). For example, generalist predators were  
68         commonly reported in various agro-ecosystems and significantly reduced pest abundance in

69 approximately 75% of cases in 181 field manipulative studies (Symondson *et al.*, 2002).  
70 Moreover, a meta-analysis suggests that generalist predators may exert stronger biocontrol  
71 effects on pest populations over time compared to specialists (Stiling and Cornelissen, 2005).

72         While the value of generalist predators has been increasingly appreciated, a few  
73 fundamental knowledge gaps need to be filled to validate their biocontrol potential and the  
74 underlying mechanisms in agro-ecosystems. For example, while studies have qualitatively  
75 analyzed the diets of generalist predators (e.g., using molecular gut content analysis to identify  
76 prey species) (Eitzinger and Traugott, 2011; Ingrao *et al.*, 2017; Albertini *et al.*, 2018), very few  
77 have quantified their diet composition over a growth season in the field (knowledge gap 1) (Hsu  
78 *et al.*, 2021; Otieno *et al.*, 2023). Quantifying their diet composition will help address the  
79 concern that generalist predators may switch their diet from pests to alternative prey and thus  
80 reduce their pest control effectiveness (Michalko *et al.*, 2019). For instance, if generalist  
81 predators still consume a high proportion of pests in their diet with the presence of alternative  
82 prey in the field, this result would help end a long debate on whether generalist predators serve  
83 well as biocontrol agents (Symondson *et al.*, 2002; Krey *et al.*, 2017; Michalko *et al.*, 2019).  
84 Moreover, examining the consistency of generalist predators in pest consumption in the field  
85 over years is important to assess the reliability of these predators as biocontrol agents in  
86 agriculture, although this information is lacking (knowledge gap 2). Given that temporal  
87 dynamics in population density or species composition commonly occur in agro-ecosystems  
88 (Settle *et al.*, 1996; Dominik *et al.*, 2018), a consistently high pest consumption by generalist  
89 predators over years, if it occurs, will provide strong support for applying these predators in pest  
90 management programs.

91 To understand the underlying mechanisms for the biocontrol effect of generalist predators,  
92 we also need to examine how various abiotic and biotic factors affect the diet composition of  
93 generalist predators in agro-ecosystems (knowledge gap 3). First, arthropod community  
94 composition (e.g., pest vs. alternative prey density) may vary with crop stages and affect  
95 predator-prey trophic interactions (Roubinet *et al.*, 2017). Therefore, we should examine how  
96 crop stage affects the pest consumption by generalist predators within a growth season. Second,  
97 we should examine whether farming practices (e.g., organic and conventional) influence the diet  
98 composition of predators (e.g., pest consumption) (Birkhofer *et al.*, 2011). This will demonstrate  
99 whether generalist predators provide varying biocontrol values in specific farm types. Third, we  
100 should investigate the relationship between the relative prey abundance and the diet composition  
101 of their predators. This will clarify whether pest abundance or predator preference mainly  
102 explains the pest consumption by predators (Wise *et al.*, 2006; Kuusk and Ekbom, 2012;  
103 Roubinet *et al.*, 2017; Eitzinger *et al.*, 2019). Lastly, we should examine how surrounding  
104 vegetation (e.g., forest cover) affects the diet composition of generalist predators. While  
105 surrounding vegetation reportedly affected arthropod diversity and predator-prey interactions in  
106 agro-ecosystems (Altieri and Letourneau, 1982; Altieri, 1999; Barbosa and Castellanos, 2005;  
107 Diehl *et al.*, 2013; Lichtenberg *et al.*, 2017), its effect on predators' diet composition is unclear.  
108 Understanding this will provide insights for managing the agricultural landscape and promoting  
109 biocontrol services by generalist predators.

110 To address these three knowledge gaps, this study aimed to 1) quantify the diet  
111 composition of generalist predators, 2) examine the consistency of predators in pest consumption  
112 over years, and 3) investigate how abiotic and biotic factors may affect the diet composition of  
113 these predators. Filling these gaps will provide insights for applying generalist predators in

114 biocontrol programs. Specifically, this study sampled arthropod prey and generalist arthropod  
115 predators (GAPs) in sub-tropical organic and conventional rice farms over the rice growth season  
116 (seedling, tillering, flowering, and ripening stages) in central Taiwan from 2017 to 2019, and  
117 quantified the diet composition of GAPs (ladybeetles and spiders) at each rice stage using stable  
118 isotope analysis ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ). Although GAPs may consume various prey items, we expected  
119 that GAPs would consistently consume a high proportion of pests in their diet at late crop stages  
120 (with high pest densities) regardless of years. We also expected that the diet composition of  
121 GAPs would be affected by local abiotic and biotic factors (e.g., farm type, crop stage, percent  
122 forest cover, and the relative abundance of pests in the field). Stable isotope analysis has been  
123 widely applied in ecology to infer predator-prey trophic interactions and estimate the  
124 proportional contribution of different prey sources to predators' diets (Post, 2002; Boecklen *et al.*,  
125 2011; Layman *et al.*, 2012). This quantification method reflects accumulated prey consumption  
126 in predators' diets, which may not be achieved by some "snap-shot" techniques (e.g., field  
127 observations and molecular gut content analysis) (Newton, 2016).

128

## 129 **2. Materials and Methods**

### 130 *2.1. Study system and sample collection*

131 We collected terrestrial arthropods in paired organic and conventional rice farms in  
132 subtropical Taiwan (120.656-120.721 °E; 24.364-24.489 °N) from 2017 to 2019 (three farm  
133 pairs in 2017 and seven farm pairs each in 2018 and 2019). While farms in the same pair were  
134 relatively close to each other (e.g., within a few hundred meters in distance), different farm pairs  
135 were at least 1 km apart from each other to reduce confounding effects. The study farms were  
136 0.2 hectares on average and irrigated with surface water. The organic farms were managed with

137 organic fertilizers (manure; 2-3 applications/crop season) and natural pesticides (tea saponins; 1  
138 application/crop season during the seedling or tillering stage). The conventional farms were  
139 managed with synthetic nitrogen fertilizers (2-3 applications/crop season) and organophosphate  
140 pesticides (1 application/crop season during the tillering or flowering stage). At each major rice  
141 crop stage (seedling, tillering, flowering, and ripening stages) during the growing season (April -  
142 July) in each study year, we collected arthropod samples by sweep-netting (36 cm in diameter  
143 with a mesh size of 0.2 × 0.2 mm) the crop canopy 30 times in each of two transects inside a rice  
144 field. Each transect (ca 30 m long) was parallel to but 1.5m away from a randomly selected farm  
145 ridge. Samples were sealed in bags without chemical preservatives, iced, and transferred to  
146 refrigerator (-20°C) in the laboratory. We identified and counted arthropods under a dissecting  
147 scope to the lowest possible taxonomic level (usually species, genus, or family). Main orders,  
148 families, and genera have been documented in Hsu et al. (Hsu *et al.*, 2021).

149

## 150 2.2. *Stable isotope analysis of arthropod samples*

151 After identification, arthropod samples were prepared for stable isotope analysis. First,  
152 samples were oven dried (50°C) for one week, ground, and weighed into individual tin capsules  
153 (5 × 9 mm). If necessary, several conspecifics would be pooled into a capsule to meet the  
154 minimum weight required for stable isotope analysis (i.e., 2 mg in this study). Stable isotope  
155 analysis (352 arthropod predator and 828 prey isotope samples) was conducted at the UC Davis  
156 Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ  
157 Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The standards for  
158 carbon and nitrogen stable isotope ratios were Vienna PeeDee Belemnite and atmospheric N<sub>2</sub>,

159 respectively. The results of our samples were expressed in per mil (‰) relative to the  
160 international standards ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ).

161

162 *2.3. Arthropod trophic guild assignment*

163 A trophic guild represents a group of species using similar resources and forms a basic  
164 component of food webs. The concept has been proved to be practical in current ecology  
165 because it condenses broad taxonomic information into distinct functional groups in  
166 communities (Blondel, 2003). In this study, we classified arthropod samples into four trophic  
167 guilds (one predator and three prey guilds): 1) “Predators” consisted of spiders and ladybeetles,  
168 which are the primary GAPs in rice farms. 2) “Rice herbivores” consisted of major rice pests,  
169 including planthoppers, leafhoppers, and stink bugs. 3) “Tourist herbivores” consisted of  
170 herbivorous species without direct trophic association with rice plants, including some  
171 grasshoppers and leaf beetles. 4) “Detritivores” consisted of arthropods that feed on decaying  
172 organic material or plankton, including various midge and fly species. The classification of prey  
173 guilds was based on a combination of literature surveys and k-means clustering of stable isotope  
174 signatures of arthropod samples (see Appendix A: Fig. S1 for a stable isotope biplot for the three  
175 prey sources). The arthropod families/genera in each trophic guild are detailed in Appendix A:  
176 Table S1. This study focused on the trophic interactions between generalist predators and their  
177 prey sources and therefore did not consider less abundant trophic guilds (e.g., parasitoids) in  
178 subsequent analyses.

179

180 *2.4. Data analyses*

181 To quantify the diet composition of predators, we constructed Bayesian stable isotope  
182 mixing models using the R MixSIAR package (Stock and Semmens, 2016) to estimate the  
183 proportions of different prey sources (i.e., the three prey guilds including rice herbivores, tourist  
184 herbivores, and detritivores) in predators' diet. In the mixing models, individual farm-year  
185 combination and crop stage were included as fixed effects for predator isotope data; isotope data  
186 for the three prey guilds were pooled respectively to generate fixed source values because of  
187 their high mobility across farms (Mazzi and Dorn, 2012; Sun *et al.*, 2015). Isotope data at the  
188 seedling stage for the three study years were omitted from the analysis due to insufficient sample  
189 sizes for model estimation. To improve our model estimates, carbon and nitrogen concentration  
190 dependencies as well as the residual/process errors were incorporated (Phillips and Koch, 2002;  
191 Stock and Semmens, 2016). Trophic discrimination factors (TDFs) were estimated from the  
192 diet-dependent discrimination equation proposed by Caut *et al.* (2009). We ran three Markov  
193 Chain Monte Carlo (MCMC) chains, each with 50,000 iterations and a burn-in number of 25,000,  
194 along with a non-informative Dirichlet prior. Chain convergence was assessed via Gelman-  
195 Rubin and Geweke diagnostics. Bayesian posterior median estimates of diet composition (for  
196 each farm-year-stage combination) were extracted for further analyses.

197 To examine how local abiotic and biotic factors may affect the pest consumption by  
198 GAPs, we fit generalized linear models (GLMs) with a beta distribution and a logit link function  
199 using the R betareg package (Zeileis *et al.*, 2016), with year, farm type, crop stage, percent forest  
200 cover, and the relative abundance of rice herbivores as fixed effects and the proportion of rice  
201 herbivores consumed in predators' diet as the response variable (i.e., posterior medians from the  
202 Bayesian stable isotope mixing models). Model parameters were estimated using maximum  
203 likelihood, and their significance was analyzed via likelihood ratio test using the "Anova"

204 function in the R car package (Fox and Weisberg, 2018). Tukey's post-hoc tests were performed  
205 for the significant factors using the "cld" function in the R emmeans package (Lenth and Lenth,  
206 2018). The percent forest cover around each study farm was estimated from Google Earth  
207 images by manually delimiting the forested areas within a 1-km radius circular buffer  
208 surrounding the farm and computing the fraction of these areas in the buffer zone. The 1-km  
209 radius was based on previous studies (Rusch et al., 2016). Because spiders and ladybeetles  
210 exhibited distinct foraging behavior (e.g., sit-and-wait vs. active hunting), we also performed all  
211 the aforementioned analyses separately for each of the two predator groups. All analyses were  
212 conducted in R version 4.0.3 (R Core Team, 2021).

213

### 214 **3. Results**

#### 215 *3.1. Diet composition of predators in rice farms*

216 Across organic and conventional farms during 2017-2019, the proportion of rice  
217 herbivores in predators' diet increased over the course of the crop season from 21-47% at the  
218 tillering stage to 80-97% at the ripening stage; the proportion of detritivores in predators' diet  
219 decreased from 35-61% at the tillering stage to <1% at the ripening stage; the proportion of  
220 tourist herbivores in predators' diet also decreased from 13-20% at the tillering stage to 3-18% at  
221 the ripening stage (Fig. 1a; Appendix A: Table S2, Fig. S2).

222 Regarding individual predator groups, spiders and ladybeetles showed a marked  
223 difference in their diet composition over crop stages during 2017-2019. Across organic and  
224 conventional farms, spiders consumed a higher proportion of detritivores (31-55%) in their diet  
225 in the beginning of crop season (tillering stage) and substantially increased the consumption on  
226 rice herbivores to 78-95% in late crop season (ripening stage) (Fig. 1b; Appendix A: Table S2,

227 Fig. S2). In contrast, ladybeetles in both organic and conventional farms consumed a low  
228 proportion of detritivores ( $\leq 8\%$ ) and a steadily high proportion of rice herbivores ( $\geq 80\%$ ) in  
229 their diet throughout the crop season (Fig. 1c; Appendix A: Table S2, Fig. S2). Tourist  
230 herbivores generally did not constitute an important prey source and contributed less than 33% to  
231 the diet of spiders and ladybeetles (Fig. 1b, 1c; Appendix A: Table S2, Fig. S2).

232

233 *3.2. Patterns of rice herbivore consumption by predators*

234 We further analyzed rice herbivore consumption by GAPs since these herbivores are the  
235 main pests of concern. The patterns of rice herbivore consumption by both predators in organic  
236 and conventional rice farms were generally similar across the three study years, suggesting  
237 consistency in GAPs' feeding habits (Fig. 2). The consistency in herbivore consumption over  
238 years was also revealed by our beta regression model, which indicated that the proportion of rice  
239 herbivores consumed in all predators' diet did not vary across years ( $\chi^2 = 2.02, P = 0.36$ ; Table  
240 1).

241 Interestingly, spiders and ladybeetles exhibited distinct within-season patterns of rice  
242 herbivore consumption. For spiders in organic and conventional farms, the proportion of rice  
243 herbivores in their diet increased toward later crop season, ranging from 17-48% (tillering) to 78-  
244 95% (ripening) (Fig. 2b; Appendix A: Table S2, Fig. S2), whereas for ladybeetles in organic and  
245 conventional farms, the proportion of rice herbivores in their diet remained relatively stable  
246 throughout the season, ranging from 80-93% (tilling) to 97-98% (ripening) (Fig. 2c; Appendix A:  
247 Table S2, Fig. S2).

248

249 *3.3. Factors associated with rice herbivore consumption by predators*

250           The proportion of rice herbivores in GAPs' diet differed between organic and  
251 conventional farms for both predators ( $\chi^2 = 20.18, P < 0.001$ ) and spiders ( $\chi^2 = 11.58, P < 0.001$ ),  
252 but not ladybeetles ( $\chi^2 = 1.35, P = 0.25$ ; Table 1). Specifically, both predators consumed a  
253 higher proportion of rice herbivores in their diet in conventional vs. organic farms (Tukey's post-  
254 hoc test,  $P < 0.05$ ; Table 2). The proportion of rice herbivores in GAPs' diet also differed among  
255 crop stages (both predators:  $\chi^2 = 225.48, P < 0.001$ ; spiders:  $\chi^2 = 95.93, P < 0.001$ ; ladybeetles:  
256  $\chi^2 = 90.94, P < 0.001$ ; Table 1). Specifically, GAPs consumed higher proportions of rice  
257 herbivores in their diet at the flowering and/or ripening stage vs. the tillering stage (Tukey's  
258 post-hoc test,  $P < 0.05$ ; Table 3).

259           The proportion of rice herbivores consumed in GAPs' diet was not associated with the  
260 percent forest cover within a 1-km radius buffer surrounding the study farms (both predators:  $\chi^2$   
261  $= 0.61, P = 0.43$ ; spiders:  $\chi^2 = 0.95, P = 0.33$ ; ladybeetles:  $\chi^2 = 0.76, P = 0.38$ ; Table 1).  
262 Furthermore, the proportion of rice herbivores consumed was not associated with the relative  
263 abundance of rice herbivores in the field (both predators:  $\chi^2 = 0.08, P = 0.77$ ; spiders:  $\chi^2 = 0.92,$   
264  $P = 0.34$ ; ladybeetles:  $\chi^2 = 1.15, P = 0.28$ ; Table 1).

265

#### 266   **4. Discussion**

267           Because the worldwide demand for environmentally friendly practices in agriculture has  
268 increased, we investigated the potential of GAPs (ubiquitous in nature) as biocontrol agents in  
269 agro-ecosystems. Specifically, we used stable isotopes to quantify the diet composition of GAPs  
270 in organic and conventional rice farms during the crop season in three consecutive years. Our  
271 main results include the following: 1) Across the three study years, the rice herbivore  
272 consumption by GAPs increased in both organic and conventional farms over the crop season,

273 from 20-47% at the tillering stage to 80-97% at the ripening stage (Fig. 1a). The high percentage  
274 at the ripening stage indicates that GAPs could function as specialists in pest management during  
275 critical growth (late crop) stages. Notably, rice herbivore consumption by spiders increased  
276 gradually toward the later crop season (Fig. 2b), whereas the consumption by ladybeetles  
277 remained stable throughout the season (Fig. 2c). 2) Our results revealed similar among-year  
278 patterns in rice herbivore consumption by GAPs in organic and conventional rice farms,  
279 suggesting a consistency in GAPs' feeding habits and biocontrol value (Fig. 2, Table 1). 3) The  
280 proportion of rice herbivores in GAPs' diets varied with farm type and crop stage (e.g., higher in  
281 conventional farms and during flowering/ripening stages). However, contrary to results from  
282 previous studies, pest consumption by GAPs was not associated with surrounding landscape (e.g.,  
283 percent forest cover) or the relative abundance of rice herbivores in the field (Table 1). We  
284 discuss in the following: 1) GAPs function as pest specialists at late crop stages, 2) GAPs exhibit  
285 consistent pest consumption patterns over years, 3) factors associated with pest consumption by  
286 GAPs, and 4) the potential caveats of this study (e.g., pest suppression and intraguild predation).  
287 We finish by highlighting the implications of our results for agricultural management.  
288

#### 289 *4.1. Generalist predators function as pest specialists at late crop stages*

290 While biocontrol, a farming practice with a long history, offers a promising solution for  
291 sustainable agriculture, the use of GAPs as biocontrol agents remains a concern because GAPs  
292 may switch diets between pests and alternative prey (Albajes and Alomar, 1999; Prasad and  
293 Snyder, 2006; Roubinet *et al.*, 2018). This study addressed this concern and revealed a  
294 consistency in high pest consumption by GAPs at late crop stages over years. The results  
295 provide not only strong support for using GAPs in sustainable pest management, but also a novel

296 aspect in biocontrol—generalist predators may function as guild-level specialist predators of  
297 pests during the late crop season. Specifically, across the three study years, GAPs in both  
298 organic and conventional farms consumed an increasing proportion of rice herbivores over the  
299 crop season, reaching 80-97% in predators' diet at the ripening stage, whereas the proportions of  
300 alternative prey (detritivores and tourist herbivores) in their diet gradually decreased below 18%  
301 at the ripening stage (Fig. 1; Appendix A: Table S2, Fig. S2). The increase in rice herbivore  
302 consumption over time suggests that the biocontrol potential of predators increases toward late  
303 crop stages and peaks at the critical stage of crop production. This could be because of a higher  
304 herbivore (pest) density at late crop stages, suggested by a correlation between rice herbivore  
305 consumption and crop stage (see *Factors associated with pest consumption by predators*).

306 While GAPs consumed a high proportion of pests at late crop stages, the two predator  
307 groups in our study system, spiders and ladybeetles (Table S1), exhibited distinct dietary patterns  
308 over the crop season (Fig. 1, Fig. 2). Specifically, pest consumption by spiders increased  
309 substantially, but pest consumption by ladybeetles remained stable over the season (Fig. 2b vs.  
310 2c). This may be because different foraging modes—sit-and-wait (spiders) or actively hunting  
311 (ladybeetles)—can lead to different prey capture and thus diet composition (Nyffeler, 1999;  
312 Klecka and Boukal, 2013). For example, long-jawed orb-weavers (*Tetragnatha*), the most  
313 abundant genus in our spider samples, are sit-and-wait predators. The diet composition of these  
314 predators generally reflects prey availability (Nyffeler, 1999). In contrast, ladybeetles are  
315 actively hunting predators and may preferentially feed on rice herbivores, resulting in stable pest  
316 consumption over time (Fig. 1c, Fig. 2c, Fig. 3). Because predator foraging modes shape  
317 predator-prey-plant interactions (Schmitz, 2008), we encourage future studies to examine

318 different assemblages of sit-and-wait vs. actively hunting predators in field conditions to reveal  
319 the most efficient biocontrol practice over the entire crop season.

320

321 *4.2. Generalists exhibit consistent pest consumption patterns over years*

322        Ideal biocontrol agents provide a consistent, predictable effect on pests under various  
323 environmental conditions. Accordingly, GAPs in this study showed consistent pest consumption  
324 across years (Fig. 2), despite various abiotic and biotic environmental conditions. Specifically,  
325 regarding the abiotic factors, the daily mean temperature, particularly from April to June, varied  
326 substantially among years (Appendix A: Fig. S3). The daily precipitation also fluctuated over  
327 the three study years, with multiple high precipitation events in 2017, overall low precipitation in  
328 2018, and relatively uniform precipitation in 2019 (Appendix A: Fig. S3). Regarding the biotic  
329 factors, the composition of rice herbivores at the flowering and ripening stages differed  
330 substantially among the three years, in particular the two most dominant groups: leafhoppers  
331 (Cicadellidae/*Nephrotettix*) and planthoppers (Delphacidae/*Nilaparvata*) (Appendix A: Table S3).  
332 Although both abiotic and biotic factors varied substantially over the years of our study, pest  
333 consumption by GAPs generally remained stable, suggesting that GAPs can be a predictable,  
334 valuable tool for pest control in sustainable agriculture (but see Eitzinger *et al.*, 2021).

335

336 *4.3. Factors associated with pest consumption by predators*

337        The proportion of rice pests in GAPs' diets differed between farm types and among crop  
338 stages but was not associated with the percent forest cover surrounding the farms or the relative  
339 abundance of rice herbivores in the field (Table 1). Overall, GAPs in conventional farms  
340 consumed a higher proportion of rice pests in their diet compared to those in organic farms

341 (Table 2). There are two explanations for this: 1) Organic farming may promote arthropod  
342 diversity and therefore distract predators from feeding on target pests (Bengtsson *et al.*, 2005;  
343 Birkhofer *et al.*, 2008; Lichtenberg *et al.*, 2017). 2) Pest densities may be higher in conventional  
344 farms (Porcel *et al.*, 2018), leading to higher predator-prey encounter rates and thus pest  
345 consumption by GAPs. Regardless of the potential mechanisms, our results highlight the  
346 important but overlooked biocontrol value of GAPs in conventional farming systems.

347         Besides farming practices, crop stages also affected pest consumption. Overall, pest  
348 consumption by GAPs increased from early (tillering) to late (ripening) stages (Fig. 2, Table 3),  
349 consistent with previous studies where predators consumed more pests in the late crop season  
350 (Roubinet *et al.*, 2017; Hsu *et al.*, 2021). This may be because pest populations increased with  
351 rice development and eventually predominated, leading to high pest consumption by GAPs at the  
352 flowering and ripening stages (Fig. 2 and 3). These findings indicate a higher biocontrol value of  
353 predators when the crop production is most vulnerable to pest damage. Therefore, farming  
354 practitioners may want to avoid practices that harm predators (e.g., chemical applications) during  
355 this period to maintain healthy predator populations and associated ecosystem services.

356         Complex habitat structure (e.g., surrounding vegetation) has been suggested to promote  
357 predator abundance and diversity (Langellotto and Denno, 2004; Diehl *et al.*, 2013), but such  
358 higher complexity did not affect predators' diet composition in our study (Table 1). This might  
359 be because the prey species in our study system were mostly associated with rice plants but not  
360 the surrounding vegetation, consistent with a meta-analysis where habitat complexity had no  
361 effect on crop herbivore densities (Langellotto and Denno, 2004). Furthermore, although the diet  
362 composition of generalist predators may correlate with prey availability in the field (Wise *et al.*,  
363 2006; Hsu *et al.*, 2021), our beta regression models suggest no such correlation between rice

364 herbivores and GAPs (Table 1). An explanation is that the relative abundance of rice herbivores  
365 was highly correlated with crop stage, a significant factor likely associating with various  
366 covariates (e.g., rice plant height) and explaining most variations in pest consumption by GAPs  
367 (Fig. 3, Table 1). We encourage further experiments, both observational and manipulative, to  
368 clarify the link between prey availability and generalist predators' diet composition in the field.

369

370 *4.4. Potential caveats of this study*

371 Our study demonstrates high pest consumption by GAPs in rice fields over three years  
372 and examines the factors influencing GAPs' diet composition. While our study provides  
373 evidence for GAPs' biocontrol potential, some caveats may exist. First, high pest consumption  
374 in GAPs' diets does not necessarily imply a strong suppression of pest populations in the field,  
375 since pest population dynamics depend not only on the per capita effect of predators but also  
376 predator density and diversity (Letourneau *et al.*, 2009; Rusch *et al.*, 2016). To unveil the  
377 connection between per capita pest consumption and overall pest dynamics, future work may  
378 require complementing stable isotope analysis with field observations of predator and pest  
379 populations. Furthermore, future work may examine crop damage and production to reveal the  
380 effect of GAPs on pest control and crop performance. Second, while intra-guild predation  
381 potentially influences the pest control by GAPs (Straub *et al.*, 2008; Michalko *et al.*, 2019), it  
382 was not quantified in our diet composition analysis due to the limitation of stable isotope mixing  
383 models (Hsu *et al.*, 2021). However, this may not be a major concern in our study because rice  
384 plants grow in dense clumps and form a complex structure that could substantially relax intra-  
385 guild predation pressure (Finke and Denno, 2006; Janssen *et al.*, 2007). Regardless, we caution

386 that our diet estimates of predators (without predator-predator interference) might not apply to  
387 systems where intra-guild predation prevails.

388

389 **5. Conclusions**

390 While biocontrol has been recognized as a valuable tool for sustainable agriculture,  
391 whether generalist predators can serve as effective biocontrol agents in pest management remains  
392 unclear. Our study helps solve this long-standing puzzle by using stable isotope analysis to  
393 quantify the diet composition of GAPs and identifying the underlying mechanisms for enemy-  
394 pest interactions in rice farms over three consecutive years. The results show a high proportion  
395 of rice pests in GAPs' diets in both organic and conventional farms (e.g., 80-97% at the ripening  
396 stage), suggesting that these generalist predators function as "pest specialists" at late crop stages  
397 (when rice plants are fruiting and pests are abundant). The high pest consumption remained  
398 consistent across years regardless of climatic conditions, demonstrating the potential that  
399 generalist predators may produce a stable, predictable top-down effect on pests. Overall, our  
400 study lends support to applying generalist predators as biocontrol agents in both organic and  
401 conventional farms. As sustainable agriculture has become more important than ever in human  
402 history, incorporating the ubiquitous generalist predators into pest management, such as  
403 maintaining healthy populations of these predators, will likely open a promising avenue towards  
404 this goal.

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409           MY3).

410

411     **Declaration of competing interest**

412           The authors declare that they have no known competing financial interests or personal  
413           relationships that could have appeared to influence the work reported in this paper.

414

415     **Data availability**

416           Data will be made available on request.

417

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423

424     **Author contributions**

425           All authors conducted the experiments; G.-C. Hsu and C.-K. Ho designed and wrote the  
426           manuscript; G.-C. Hsu and J.-A. Ou performed the statistical analyses.

427

428 **Appendix A. Supporting information**

429       Supplementary information associated with this article can be found in the online version  
430       at doi:xxx.

431

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576

577 **Table 1.** Statistical results from GLM beta regression models for examining the effects of  
 578 abiotic and biotic factors on pest consumption by spiders, ladybeetles, and both predators.

Model	Factor	<i>d.f.</i>	$\chi^2$	<i>P</i>
Both predators	Year	2	2.02	0.36
	Farm type	1	20.18	< 0.001
	Crop stage	2	225.48	< 0.001
	Percent forest cover	1	0.61	0.43
	Relative abundance of rice herbivores	1	0.08	0.77
Spiders	Year	2	7.58	0.02
	Farm type	1	11.58	< 0.001
	Crop stage	2	95.93	< 0.001
	Percent forest cover	1	0.95	0.33
	Relative abundance of rice herbivores	1	0.92	0.34
Ladybeetles	Year	2	15.00	< 0.001
	Farm type	1	1.35	0.25
	Crop stage	2	90.94	< 0.001
	Percent forest cover	1	0.76	0.38
	Relative abundance of rice herbivores	1	1.15	0.28

579

580

581 **Table 2.** Tukey's post-hoc tests comparing the proportion of rice herbivores consumed in the  
582 diet of predators in organic and conventional rice farms. Different superscript letters indicate  
583 significant differences in the means of the posterior medians from Bayesian stable isotope  
584 mixing models ( $\alpha = 0.05$ ).

Model	Farm type	Mean ( $\pm$ SE)	Lower 2.5%	Upper 2.5%
Both predators	Organic	0.66 <sup>a</sup> ( $\pm$ 0.02)	0.62	0.69
	Conventional	0.74 <sup>b</sup> ( $\pm$ 0.02)	0.70	0.77
Spiders	Organic	0.64 <sup>a</sup> ( $\pm$ 0.02)	0.59	0.68
	Conventional	0.73 <sup>b</sup> ( $\pm$ 0.02)	0.69	0.77
Ladybeetles	Organic	0.93 <sup>a</sup> ( $\pm$ 0.01)	0.92	0.94
	Conventional	0.94 <sup>a</sup> ( $\pm$ 0.01)	0.93	0.95

585

586

587 **Table 3.** Tukey's post-hoc tests comparing the proportion of rice herbivores consumed in the  
 588 diet of predators at three crop stages (tillering, flowering, and ripening stages). Different  
 589 superscript letters indicate significant differences in the means of the posterior medians from  
 590 Bayesian stable isotope mixing models ( $\alpha = 0.05$ ).

Model	Crop stage	Mean ( $\pm$ SE)	Lower 2.5%	Upper 2.5%
Both predators	Tillering	0.30 <sup>a</sup> ( $\pm$ 0.03)	0.24	0.36
	Flowering	0.86 <sup>b</sup> ( $\pm$ 0.02)	0.82	0.89
	Ripening	0.93 <sup>c</sup> ( $\pm$ 0.01)	0.91	0.96
Spiders	Tillering	0.34 <sup>a</sup> ( $\pm$ 0.04)	0.26	0.42
	Flowering	0.83 <sup>b</sup> ( $\pm$ 0.02)	0.78	0.87
	Ripening	0.88 <sup>b</sup> ( $\pm$ 0.02)	0.83	0.93
Ladybeetles	Tillering	0.91 <sup>a</sup> ( $\pm$ 0.01)	0.89	0.92
	Flowering	0.92 <sup>a</sup> ( $\pm$ 0.01)	0.90	0.94
	Ripening	0.98 <sup>b</sup> ( $\pm$ 0.00)	0.97	0.98

591

592 **Figures (color should be used for Figure 1, 2, and 3)**

593 **Figure 1.** The proportions (mean  $\pm$  SE) of prey sources (rice herbivores, tourist herbivores, and  
594 detritivores) consumed in the diet of (a) both predators, (b) spiders, and (c) ladybeetles in organic  
595 and conventional rice farms over crop stages. The proportions were computed from the  
596 Bayesian posterior medians of diet estimates in replicate farms over the three study years.

597

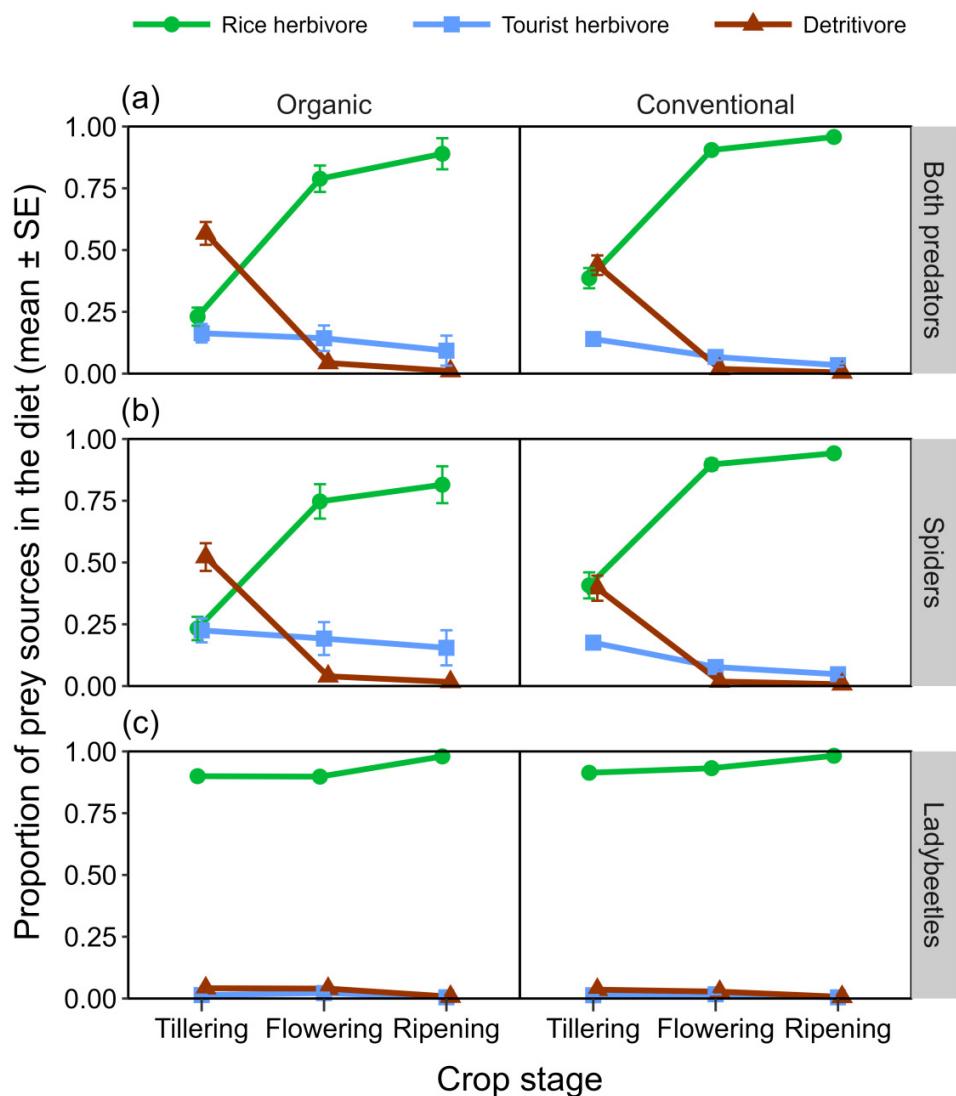
598 **Figure 2.** The proportion of rice herbivores consumed in the diet of (a) both predators, (b)  
599 spiders, and (c) ladybeetles in organic and conventional rice farms over crop stages in the three  
600 study years. The proportions were computed from the Bayesian posterior medians of diet  
601 estimates in replicate farms.

602

603 **Figure 3.** The relative abundance of prey sources in organic and conventional rice farms over  
604 crop stages during the three study years. The relative abundance was determined from the  
605 sweep-net samples pooled across replicate farms.

606

607 **Figure 1.**

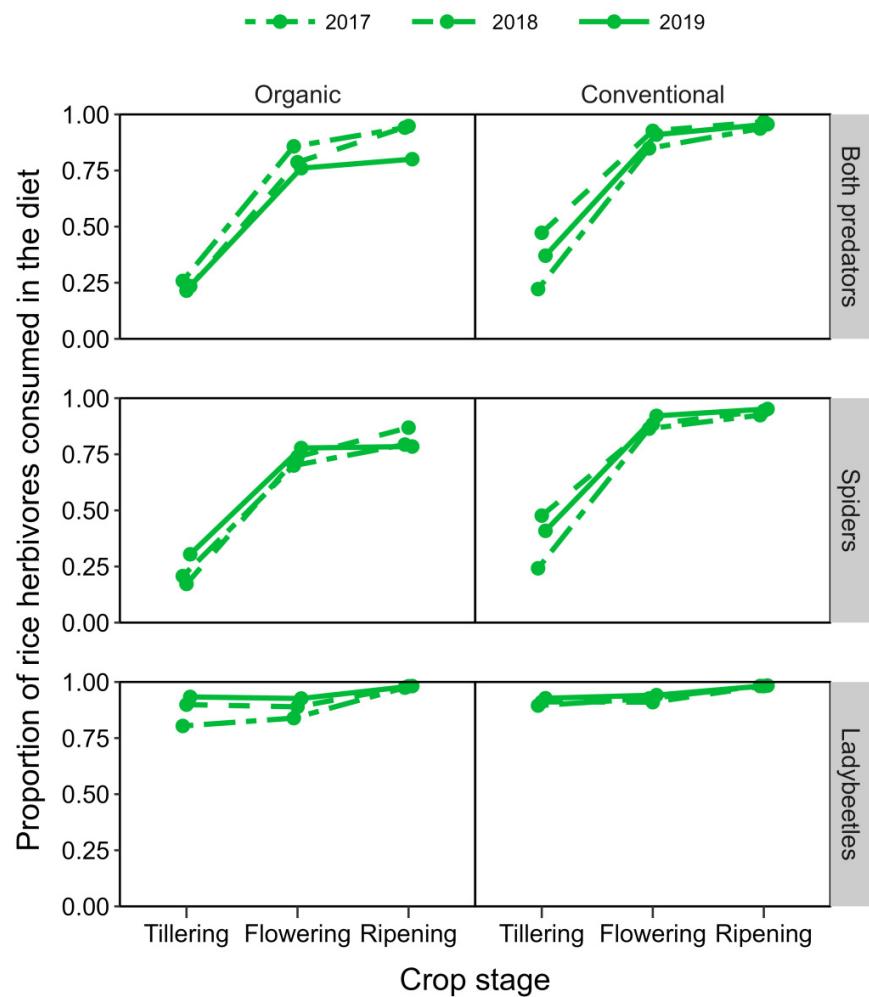


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611 **Figure 2.**

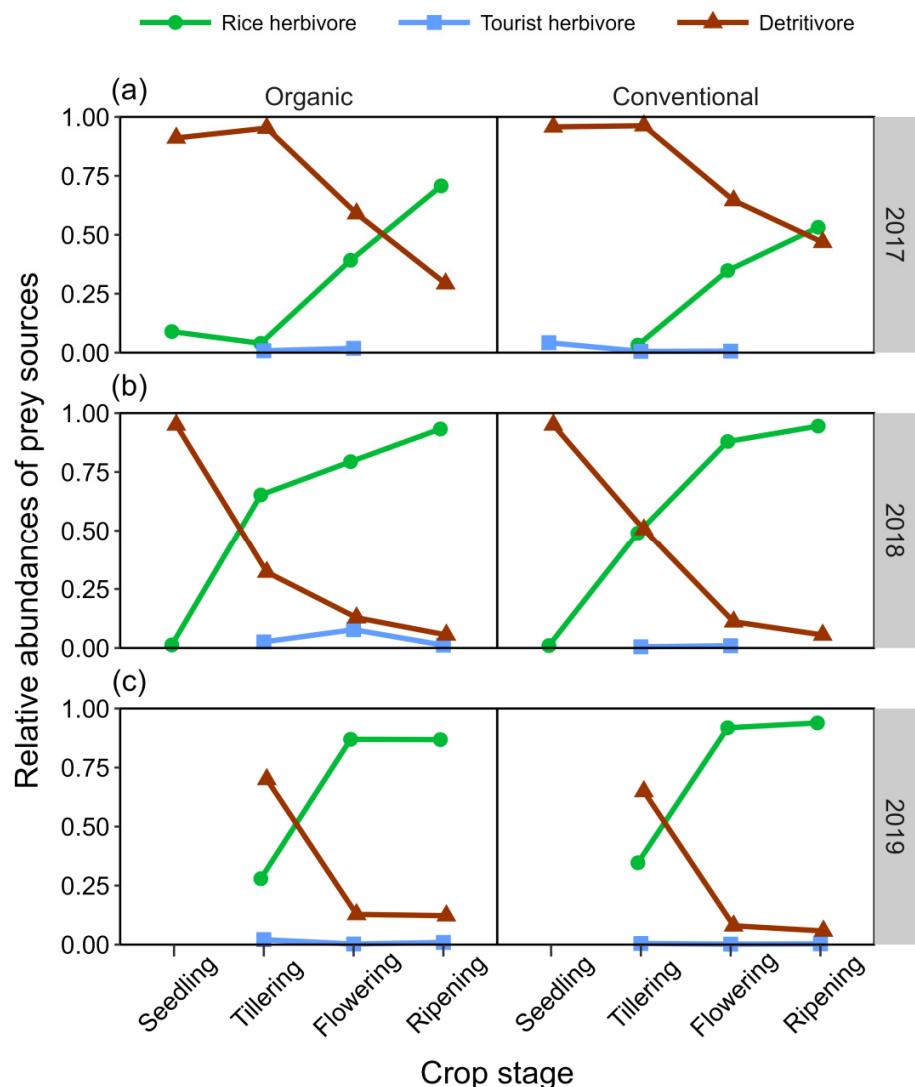


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615 **Figure 3.**



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617



1

## Appendix A.

2

### **A predator in need is a predator indeed: generalist arthropod predators function as pest specialists at the late growth stage of rice**

4

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16 **Table S1.** The taxonomic information and trophic guilds of the arthropod samples in the three  
17 study years.

18 (a) Year 2017

Trophic guild	Order	Family/Genus
Predators	Araneae	Araneidae
	Araneae	Clubionidae
	Araneae	Oxyopidae
	Araneae	Tetragnathidae/ <i>Tetragnatha</i>
	Araneae	Thomisidae
	Coleoptera	Carabidae
Rice herbivores	Coleoptera	Coccinellidae
	Hemiptera	Cicadellidae/ <i>Nephrotettix</i>
	Hemiptera	Delphacidae/ <i>Nilaparvata</i>
	Hemiptera	Lygaeidae/ <i>Pachybrachius</i>
	Hemiptera	Pentatomidae/ <i>Scutinophara</i>
	Lepidoptera	Hesperiidae
	Lepidoptera	Pyralidae
	Lepidoptera	Nymphalidae
	Orthoptera	Pyrgomorphidae/ <i>Atractomorpha</i>
Tourist herbivores	Coleoptera	Chrysomelidae
	Orthoptera	Acrididae
Detritivores	Diptera	Chironomidae
	Diptera	Chloropidae
	Diptera	Ephydriidae
	Diptera	Muscidae
	Diptera	Sphaeroceridae
	Diptera	Stratiomyidae
	Diptera	Tephritidae

19

20 (b) Year 2018

	Orthoptera	Tetrigidae
Trophic guild	Order	Family/Genus
Predators	Araneae	Araneidae
	Araneae	Clubionidae
	Araneae	Oxyopidae
	Araneae	Tetragnathidae/ <i>Tetragnatha</i>
	Araneae	Thomisidae
	Coleoptera	Coccinellidae
Rice herbivores	Hemiptera	Alydidae/ <i>Leptocoris</i>
	Hemiptera	Cicadellidae/ <i>Nephrotettix</i>
	Hemiptera	Delphacidae/ <i>Nilaparvata</i>
	Hemiptera	Lygaeidae/ <i>Pachybrachius</i>
	Hemiptera	Pentatomidae/ <i>Scotinophara</i>
	Lepidoptera	Hesperiidae
	Lepidoptera	Pyralidae
	Orthoptera	Pyrgomorphidae/ <i>Atractomorpha</i>
Tourist herbivores	Coleoptera	Chrysomelidae
	Orthoptera	Acrididae
Detritivores	Diptera	Chironomidae
	Diptera	Chloropidae
	Diptera	Ephydriidae
	Diptera	Muscidae
	Diptera	Sciomyzidae
	Diptera	Stratiomyidae
	Orthoptera	Tetrigidae

21

22 (c) Year 2019

Trophic guild	Order	Family/Genus
Predators	Araneae	Araneidae
	Araneae	Clubionidae
	Araneae	Oxyopidae
	Araneae	Tetragnathidae/ <i>Tetragnatha</i>
	Araneae	Thomisidae
	Coleoptera	Coccinellidae
Rice herbivores	Diptera	Agromyzidae
	Hemiptera	Alydidae/ <i>Leptocoris</i> a
	Hemiptera	Cicadellidae/ <i>Nephrotettix</i>
	Hemiptera	Coreidae
	Hemiptera	Delphacidae/ <i>Nilaparvata</i>
	Hemiptera	Lygaeidae/ <i>Pachybrachius</i>
	Hemiptera	Miridae
	Hemiptera	Pentatomidae/ <i>Scotinophara</i>
	Hemiptera	Ricaniidae
	Lepidoptera	Hesperiidae
	Lepidoptera	Nymphalidae
	Lepidoptera	Pyralidae
Tourist herbivores	Orthoptera	Pyrgomorphidae/ <i>Atractomorpha</i>
	Coleoptera	Chrysomelidae
Detritivores	Orthoptera	Acrididae
	Diptera	Calliphoridae
	Diptera	Chironomidae
	Diptera	Chloropidae
	Diptera	Ephydriidae
	Diptera	Lauxaniidae
	Diptera	Muscidae

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Diptera	Phoridae
Diptera	Platystomatidae
Diptera	Sarcophagidae
Diptera	Sciomyzidae
Diptera	Sphaeroceridae
Diptera	Stratiomyidae
Diptera	Tephritidae
Orthoptera	Tetrigidae
Orthoptera	Tridactylidae

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24 **Table S2.** The proportions (mean  $\pm$  SE) of prey sources (rice herbivores, tourist herbivores, and  
 25 detritivores) consumed in predators' diet in organic and conventional rice farms over crop stages  
 26 in each study year. The mean proportions were computed from the Bayesian posterior medians  
 27 of diet estimates in replicate farms;  $n$  represents the number of replicate farms. Note that the  
 28 differences in  $n$  within the same study year were due to insufficient predator samples in some  
 29 replicate farms.

Year	Farm type	Crop stage	Predator	Prey source			$n$
				Rice herbivore	Tourist herbivore	Detritivore	
2017	Organic	Tillering	Both	0.26 $\pm$ 0.08	0.15 $\pm$ 0.05	0.54 $\pm$ 0.13	3
			Spiders	0.21 $\pm$ 0.13	0.33 $\pm$ 0.17	0.44 $\pm$ 0.19	3
			Ladybeetles	0.80	0.02	0.08	1
		Flowering	Both	0.86 $\pm$ 0.03	0.09 $\pm$ 0.02	0.04 $\pm$ 0.02	3
			Spiders	0.70 $\pm$ 0.15	0.24 $\pm$ 0.16	0.04 $\pm$ 0.03	3
			Ladybeetles	0.84	0.03	0.07	1
		Ripening	Both	0.94 $\pm$ 0.01	0.04 $\pm$ 0.01	0.01 $\pm$ 0.01	3
			Spiders	0.79 $\pm$ 0.12	0.18 $\pm$ 0.12	0.02 $\pm$ 0.01	3
			Ladybeetles	0.97 $\pm$ 0.01	0.01 $\pm$ 0.00	0.01 $\pm$ 0.00	3
Conventional		Tillering	Both	0.22 $\pm$ 0.02	0.15 $\pm$ 0.05	0.60 $\pm$ 0.05	3
			Spiders	0.24 $\pm$ 0.01	0.20 $\pm$ 0.07	0.55 $\pm$ 0.08	3
			Ladybeetles	0.90	0.01	0.04	1
		Flowering	Both	0.85 $\pm$ 0.03	0.1 $\pm$ 0.03	0.03 $\pm$ 0.01	3
			Spiders	0.86 $\pm$ 0.02	0.1 $\pm$ 0.03	0.03 $\pm$ 0.01	3
			Ladybeetles	0.93 $\pm$ 0.01	0.02 $\pm$ 0.00	0.03 $\pm$ 0.00	2
		Ripening	Both	0.94 $\pm$ 0.02	0.05 $\pm$ 0.02	0.01 $\pm$ 0.00	3
			Spiders	0.92 $\pm$ 0.02	0.06 $\pm$ 0.02	0.01 $\pm$ 0.00	3
			Ladybeetles	0.98 $\pm$ 0.00	0.00 $\pm$ 0.00	0.01 $\pm$ 0.00	2
2018	Organic	Tillering	Both	0.21 $\pm$ 0.04	0.20 $\pm$ 0.07	0.54 $\pm$ 0.07	7
			Spiders	0.17 $\pm$ 0.03	0.26 $\pm$ 0.08	0.54 $\pm$ 0.08	7
			Ladybeetles	0.90 $\pm$ 0.02	0.01 $\pm$ 0.00	0.04 $\pm$ 0.01	6
		Flowering	Both	0.79 $\pm$ 0.04	0.14 $\pm$ 0.04	0.04 $\pm$ 0.01	6
			Spiders	0.74 $\pm$ 0.07	0.18 $\pm$ 0.07	0.04 $\pm$ 0.01	5

		Ladybeetles	$0.89 \pm 0.01$	$0.02 \pm 0.00$	$0.04 \pm 0.01$	3	
Conventional	Ripening	Both	$0.95 \pm 0.01$	$0.03 \pm 0.01$	$0.01 \pm 0.00$	5	
		Spiders	$0.87 \pm 0.04$	$0.09 \pm 0.02$	$0.02 \pm 0.01$	4	
		Ladybeetles	$0.98 \pm 0.00$	$0.00 \pm 0.00$	$0.01 \pm 0.00$	5	
	Tillering	Both	$0.47 \pm 0.08$	$0.12 \pm 0.02$	$0.35 \pm 0.05$	7	
		Spiders	$0.48 \pm 0.11$	$0.18 \pm 0.03$	$0.31 \pm 0.08$	7	
		Ladybeetles	$0.91 \pm 0.01$	$0.01 \pm 0.00$	$0.04 \pm 0.01$	4	
	Flowering	Both	$0.93 \pm 0.03$	$0.05 \pm 0.02$	$0.01 \pm 0.00$	6	
		Spiders	$0.88 \pm 0.05$	$0.09 \pm 0.04$	$0.01 \pm 0.01$	6	
		Ladybeetles	$0.91 \pm 0.03$	$0.02 \pm 0.00$	$0.04 \pm 0.01$	2	
2019	Organic	Ripening	Both	$0.97 \pm 0.01$	$0.03 \pm 0.01$	$0.00 \pm 0.00$	7
			Spiders	$0.94 \pm 0.04$	$0.05 \pm 0.04$	$0.00 \pm 0.00$	2
			Ladybeetles	$0.98 \pm 0.00$	$0.00 \pm 0.00$	$0.01 \pm 0.00$	5
		Tillering	Both	$0.23 \pm 0.08$	$0.13 \pm 0.06$	$0.61 \pm 0.08$	7
			Spiders	$0.30 \pm 0.10$	$0.14 \pm 0.05$	$0.54 \pm 0.09$	7
			Ladybeetles	$0.93 \pm 0.03$	$0.01 \pm 0.00$	$0.03 \pm 0.01$	3
		Flowering	Both	$0.76 \pm 0.12$	$0.17 \pm 0.12$	$0.05 \pm 0.01$	7
			Spiders	$0.78 \pm 0.15$	$0.18 \pm 0.14$	$0.04 \pm 0.01$	6
			Ladybeetles	$0.93 \pm 0.02$	$0.02 \pm 0.00$	$0.03 \pm 0.01$	3
	Ripening	Both	$0.80 \pm 0.17$	$0.18 \pm 0.16$	$0.01 \pm 0.00$	5	
		Spiders	$0.78 \pm 0.17$	$0.19 \pm 0.16$	$0.02 \pm 0.01$	5	
		Ladybeetles	$0.98 \pm 0.00$	$0.00 \pm 0.00$	$0.01 \pm 0.00$	5	
	Conventional	Tillering	Both	$0.37 \pm 0.04$	$0.15 \pm 0.05$	$0.46 \pm 0.06$	7
			Spiders	$0.41 \pm 0.06$	$0.16 \pm 0.05$	$0.42 \pm 0.08$	7
			Ladybeetles	$0.93 \pm 0.00$	$0.01 \pm 0.00$	$0.03 \pm 0.00$	2
		Flowering	Both	$0.91 \pm 0.02$	$0.06 \pm 0.02$	$0.02 \pm 0.00$	7
			Spiders	$0.92 \pm 0.02$	$0.06 \pm 0.02$	$0.02 \pm 0.01$	7
			Ladybeetles	$0.94 \pm 0.00$	$0.02 \pm 0.00$	$0.02 \pm 0.00$	6
		Ripening	Both	$0.96 \pm 0.01$	$0.04 \pm 0.01$	$0.00 \pm 0.00$	5
			Spiders	$0.95 \pm 0.02$	$0.04 \pm 0.02$	$0.01 \pm 0.00$	5
			Ladybeetles	$0.98 \pm 0.00$	$0.00 \pm 0.00$	$0.01 \pm 0.00$	3

31 **Table S3.** The relative abundance of the major families/genera in rice herbivore guild at the  
32 flowering and ripening stages in the three study years. Samples were pooled across replicate  
33 farms.

34 (a) Flowering stage

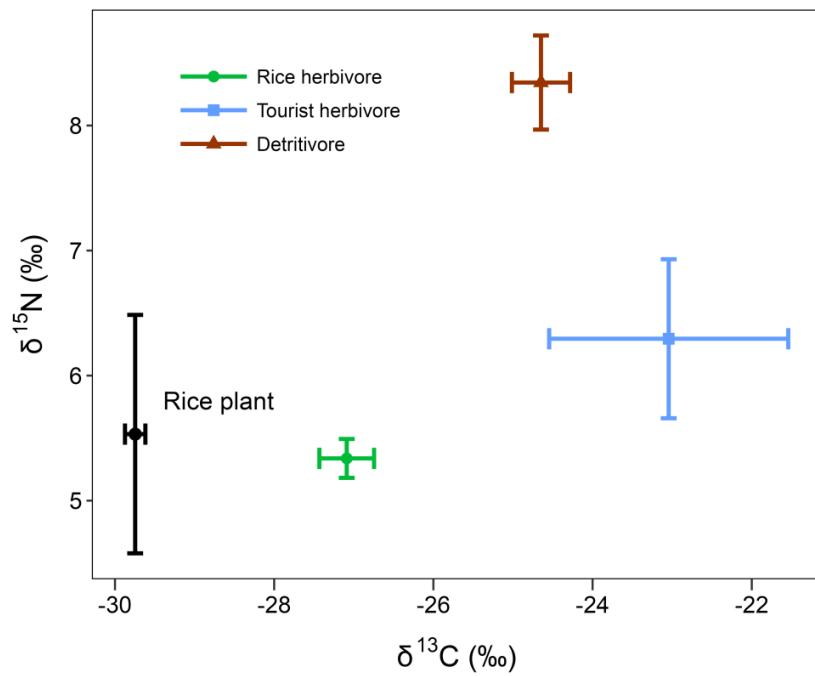
Family/Genus	Year 2017	Year 2018	Year 2019
Cicadellidae/ <i>Nephrotettix</i>	7.6%	22.5%	69.7%
Delphacidae/ <i>Nilaparvata</i>	88.2%	71.9%	25.4%
Lygaeidae/ <i>Pachybrachius</i>	NA	0.8%	1.3%
Pentatomidae/ <i>Scotinophara</i>	0.8%	2.9%	0.8%
Others	3.4%	1.9%	2.8%
<i>Total</i>	100%	100%	100%

35

36 (b) Ripening stage

Family/Genus	Year 2017	Year 2018	Year 2019
Cicadellidae/ <i>Nephrotettix</i>	69.4%	74.9%	83.5%
Delphacidae/ <i>Nilaparvata</i>	28.9%	13.4%	6.2%
Lygaeidae/ <i>Pachybrachius</i>	NA	0.2%	4.1%
Pentatomidae/ <i>Scotinophara</i>	1.7%	10.4%	4.5%
Others	NA	1.1%	1.7%
<i>Total</i>	100%	100%	100%

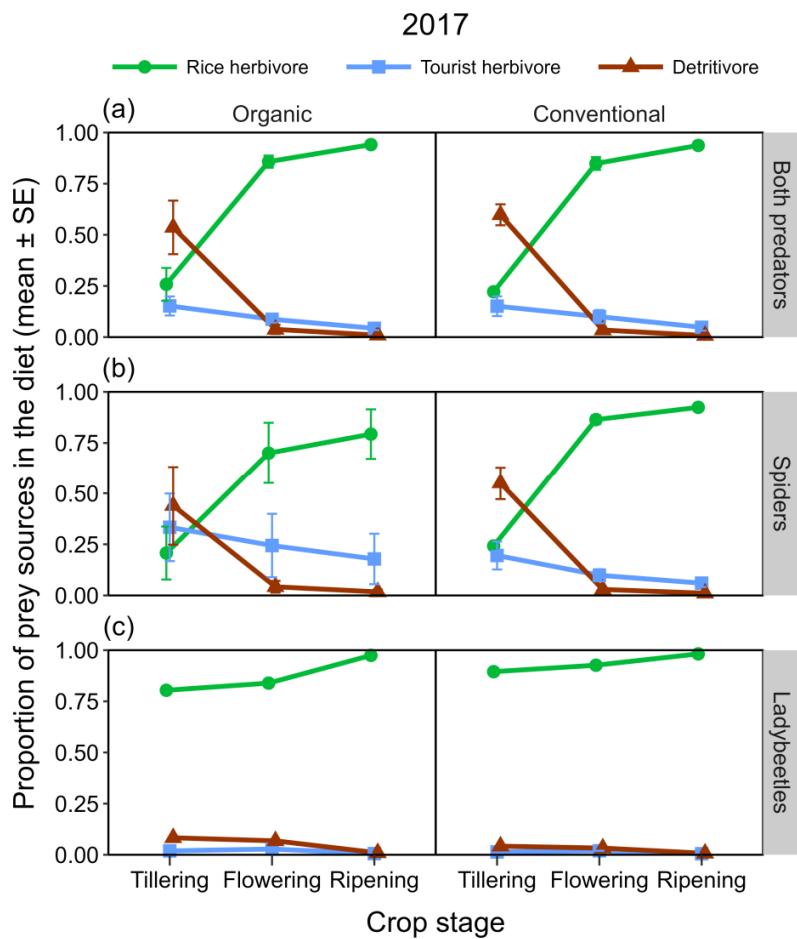
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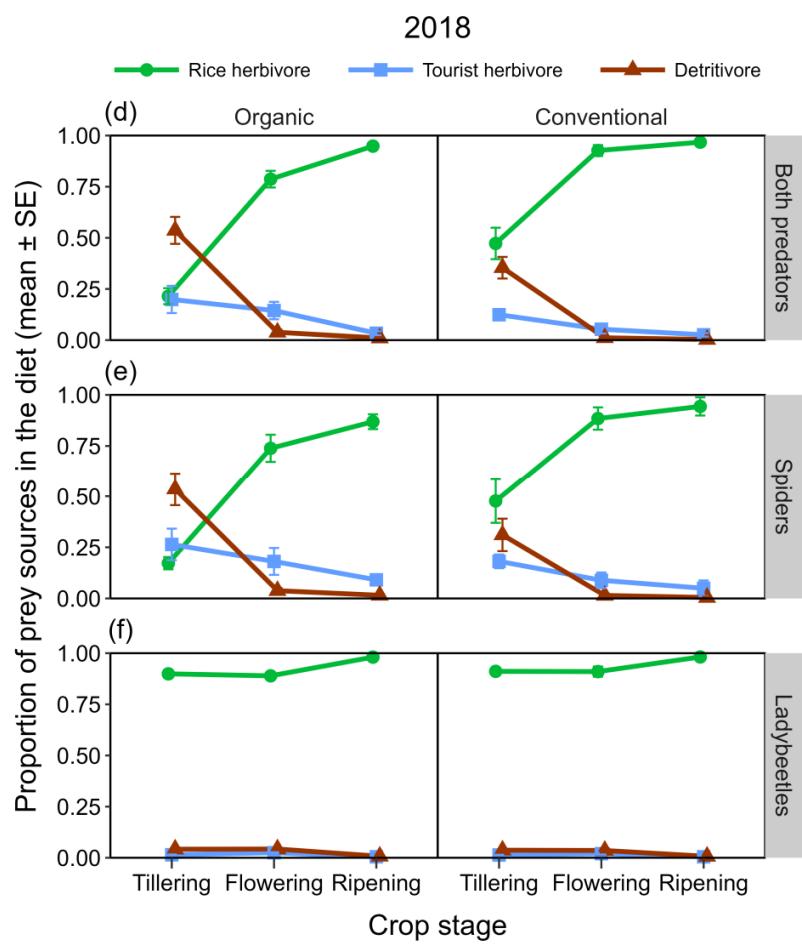
39 **Figure S1.** Stable isotope biplot of the rice plant and three prey sources in this study. Error bars  
 40 represent 95% confidence intervals.

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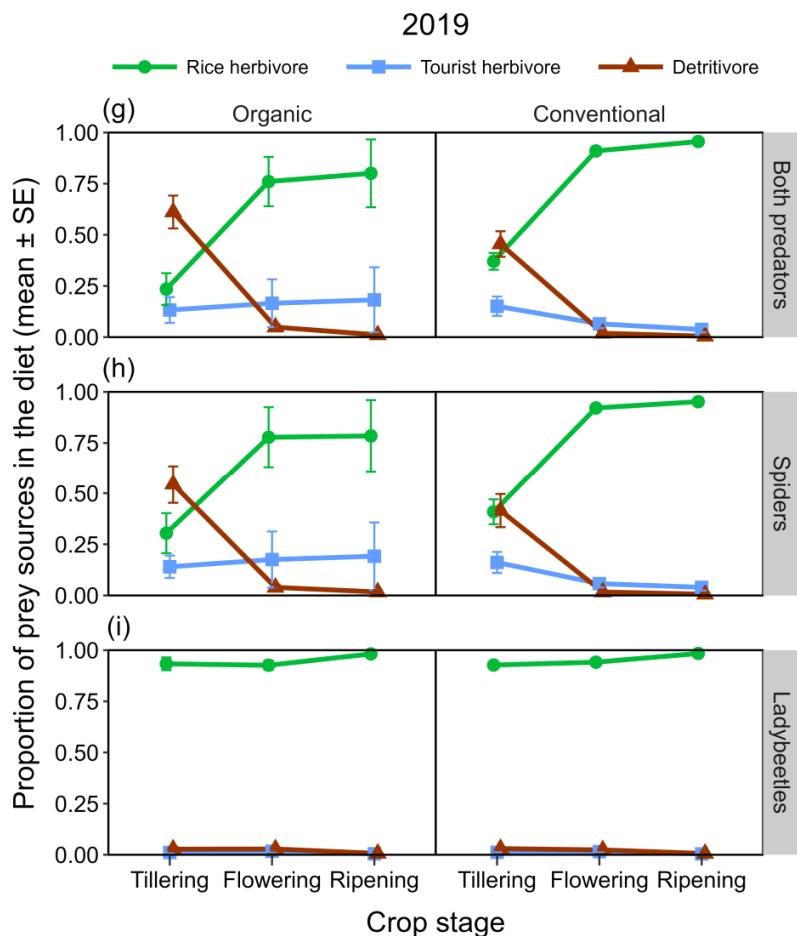
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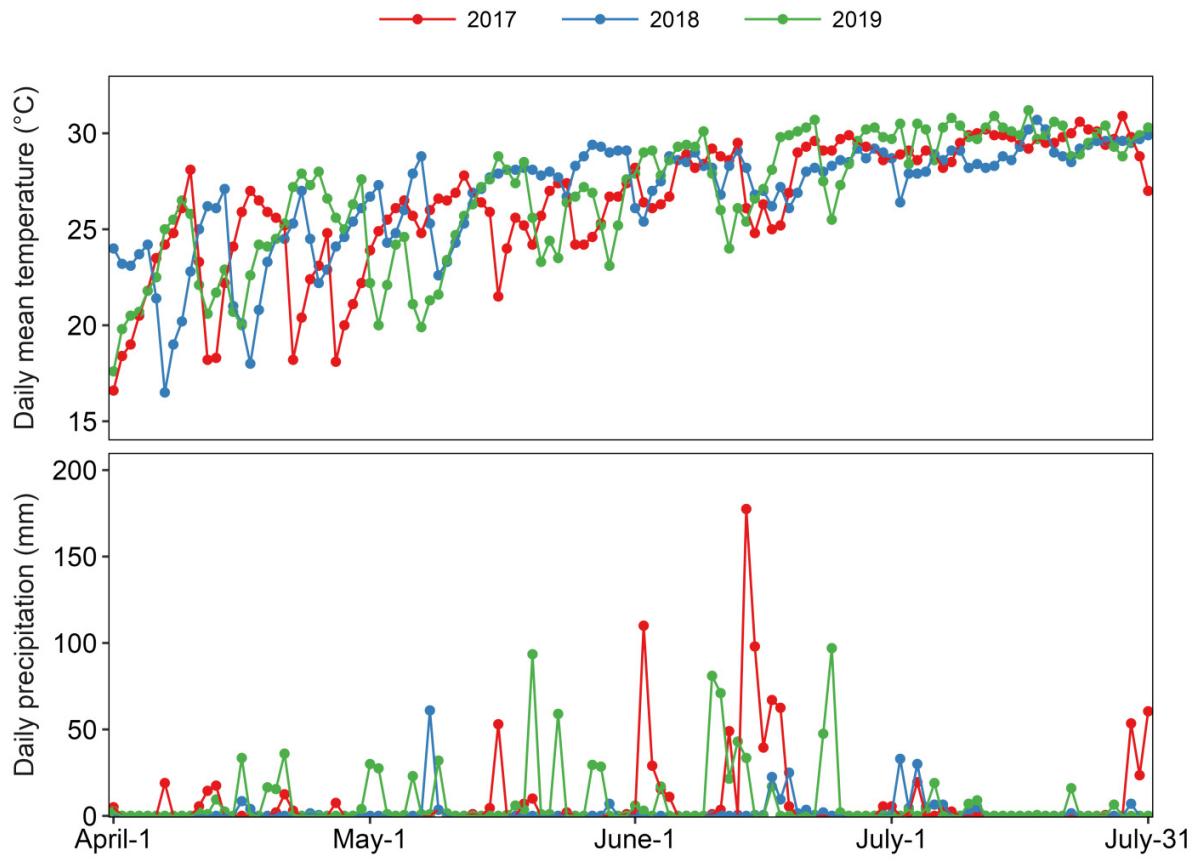
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48 **Figure S2.** The proportions (mean  $\pm$  SE) of prey sources (rice herbivores, tourist herbivores,  
49 detritivores) consumed in the diet of predators in organic and conventional rice farms over crop  
50 stages in each study year: (a), (d), and (g) indicate both predators (spiders and ladybeetles) as a  
51 whole feeding guild; (b), (e), and (h) indicate spiders; (c), (f), and (i) indicate ladybeetles. The  
52 proportions were computed from the Bayesian posterior medians of diet estimates in replicate  
53 farms.

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55

56 **Figure S3.** Daily mean temperature and precipitation of the study sites during the rice growth  
 57 season (April to July) of the three study years. Observation data from the closest local weather  
 58 station (Yuanli station) to the study farms were retrieved from the Central Weather Bureau  
 59 Observation Data Inquire System (<https://e-service.cwb.gov.tw/HistoryDataQuery/index.jsp>).

**Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: